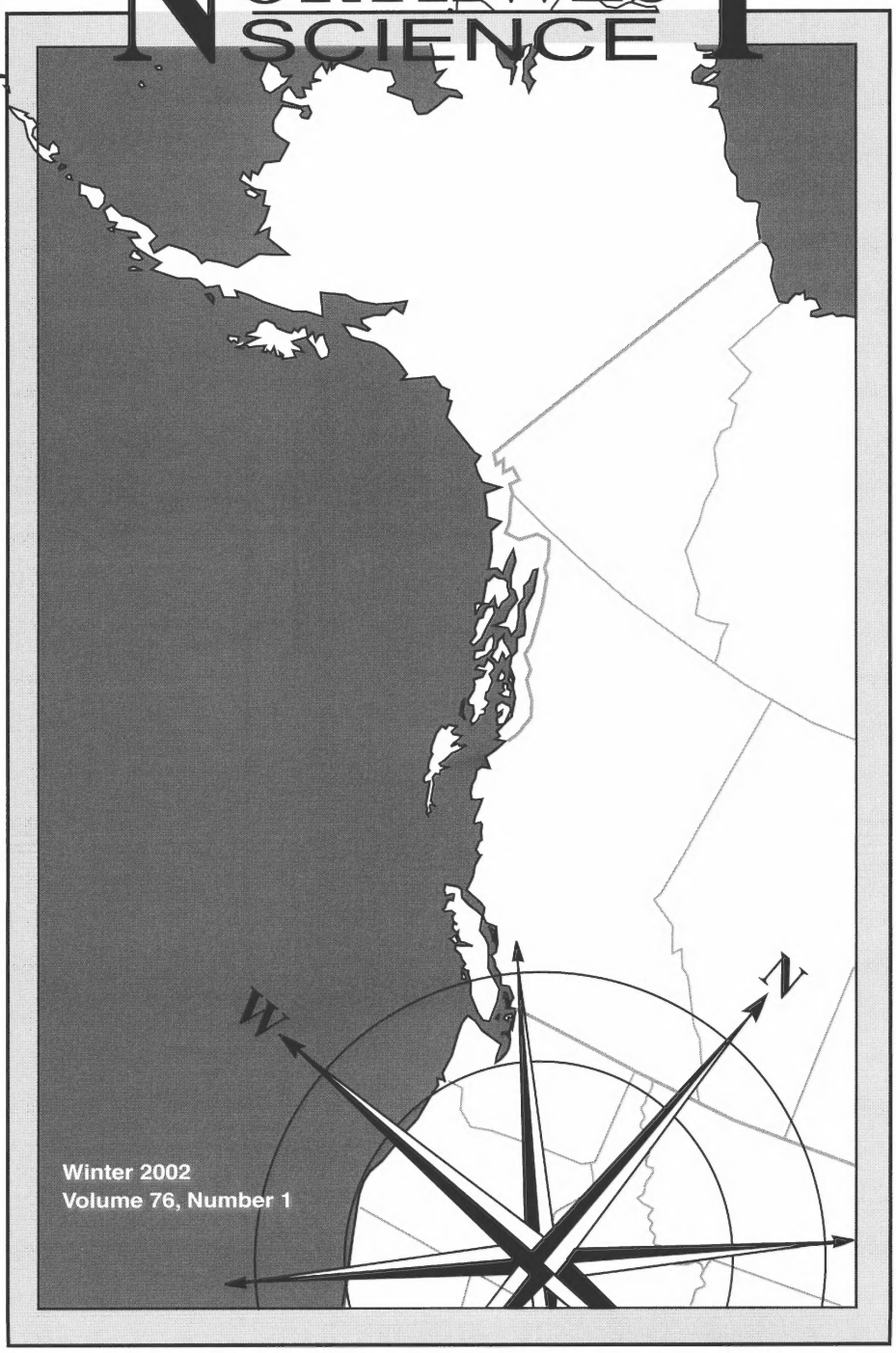
BY-LAWS

NORTHWEST SCIENCE



Winter 2002
Volume 76, Number 1

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Send changes of address and requests for undelivered issues to the Treasurer.

The Northwest Scientific Association is a 501-C(3) tax status organization.

Editor of *Northwest Science*

Rich Fonda
Biology Department
Western Washington University
Bellingham, Washington 98225
Telephone: 360-650-6599
Fax: 360-650-3148
Internet: fonda@biol.wwu.edu

Officers of the Association

President Tim Reynolds
Environmental Science and Research Foundation
Idaho Falls, Idaho (2002)*

Past President Theodore B. Thomas
USDI Fish & Wildlife Service
Olympia, Washington (2000)

Secretary Margaret O'Connell
Department of Biology MS-72
Eastern Washington University
Cheney, Washington 99004

Treasurer David H. Hansen
Department of Biology
Pacific Lutheran University
Tacoma, Washington 98447
Telephone: 253-535-7565
Fax: 253-536-5055
Internet: hansendh@plu.edu

Book Review Editor
Randall C. Morris
Environmental Science and Research Fndn.
101 S. Park Ave./PO Box 51838
Idaho Falls, ID 83405-1838
Telephone: 208-525-7053, Fax: 208-525-7036
e-mail: morrisr@esrf.org

*Term of office expires in the year given in parentheses.

Trustees:

Steve Acker
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Boise, Idaho (2003)

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USDA PNW Research Station
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Wenatchee Valley College
Wenatchee, Washington (2003)

Paul Verrell
Washington State University
Pullman, Washington (2003)

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Winter 2002 **Volume 76, Number 1**

NORTHWEST SCIENCE

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ISSN #0029-344X

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2002 Annual Meeting, Boise State University, 27-30 March

The 75th Annual Meeting of the Northwest Scientific Association will occur on the campus of Boise State University, Boise, Idaho, from Wednesday, 27 March through Saturday, 30 March, 2002. Special ceremonies to recognize the 75th meeting are being organized. Interested readers, especially those who wish to submit papers to be presented, should contact the NWSA web site for more information. A variety of scientific sessions, workshops, and field trips will be held in conjunction with the meeting. An important theme of the meeting will be the use and value of natural areas and ecological reference areas in conservation, ecological research, and teaching. Individuals interested in helping to organize sessions or workshops should contact Steve Rust, Conservation Data Center, Idaho Department of Fish and Game, P. O. Box 25, Boise, ID, 83707. Phone: 208-334-3402. FAX: 208-334-2114. E-mail: srust@idfg.state.id.us

2002 Student Research Grants

The Northwest Scientific Association annually awards grants of up to $1000 to support student research. Applicants must be student members of the Northwest Scientific Association (see inside front cover of *Northwest Science* for membership application information). Four copies of the proposal must be received on or before 1 February 2002, and sent by surface mail to:

Dr. A. Ross Black
Department of Biology (Sci 258)
526 5th Street
Eastern Washington University
Cheney, WA 99004

Proposals should include (in the following order): 1) a cover page that provides the project title, name and address of the student applicant (including phone number and e-mail address), name of the major professor or advisor, and the dollar amount requested; 2) an itemized budget ($1000 max.); 3) the body of the proposal that provides a specific statement of the project goal(s), the background, justification, appropriate preliminary results, and the project methods (including experimental design, methodologies, appropriate statistical analyses, and timeline); 4) literature cited; and 5) supplementary tables and figures. The body of the proposal is limited to no more than four pages of double spaced text in 12-pt font with one inch margins (excluding title page, budget, literature cited, and supplementary tables and figures).

Awards provided by the Northwest Scientific Association support student researchers in the pure and applied sciences. Monies can only be used to support travel, equipment, and supplies for student research (proposals requesting salary support will not be considered). Recipients are required to present the results of their research at a future Northwest Scientific Association annual meeting. NWSA will waive page charges if grant recipients choose to publish their research in *Northwest Science* within four years of accepting their grant. Grant winners will be announced at the 2002 NSA annual meeting at Boise State University, March 2002. Questions concerning grant application procedures should be directed to Dr. Ross Black via e-mail (rblack@ewu.edu).

Call for Nominations

Members may submit suggestions for nominees for trustees, secretary, and treasurer of the Board of Trustees of the Northwest Scientific Association to the Chair of the Nominations Committee Joanna Schultz according to the instructions on the NWSA web page.

New Forestry Associate Editor

Dr. David Wallin is the new Associate Editor for Forestry. David is an Associate Professor in the Department of Environmental Sciences and Huxley College of the Environment at Western Washington University. His research focuses on the regional-scale study of land-use effects on the structure and function of forest ecosystems. His work depends heavily on the use of simulation models, satellite remote sensing, and GIS. He teaches advanced courses in landscape and ecosystem ecology, and remote sensing.

Revised By-Laws

The fall meeting of the Board of Trustees of the Northwest Scientific Association was held by teleconference on 12 October 2001. At that meeting, the Board unanimously approved the following revision of the By-Laws of the Association. The revised By-Laws will be presented to the membership for vote and approval at the Annual Meeting in Boise, Idaho, 27-30 March 2002. Submit any comments regarding By-Laws no later than 1 March 2002 to Tim Reynolds, President, Northwest Scientific Association, c/o TREC, Inc., 101 S. Park Avenue, Suite 5, Idaho Falls, ID 83405.

BY-LAWS
of
Northwest Scientific Association, Inc.

ARTICLE I
NAME

The name of the Corporation shall be the Northwest Scientific Association, Inc.

ARTICLE II
PURPOSE

The association, a scientific society, is a non-profit organization whose object shall be to fund, promote, cultivate, sponsor, and develop the appreciation of scientific research in western North America.

ARTICLE III
MEMBERSHIP

Any person or organization who has paid membership dues to the society within the past year is admitted to membership in the association. Any individual member may attend the annual meeting and may vote for Directors standing for election or other business requiring vote .

Membership in this association shall consist of the following categories:

- Member: Any individual interested in the purpose of the Association may become an individual member upon payment of annual dues. Members have all privileges including voting, holding office, and receiving *Northwest Science*.
- Student Member: Any high school or college student may become a member of the Association upon the payment of annual student membership dues. Student members shall receive *Northwest Science* and will have all privileges of membership.
- Institutional Member: Available to all universities, colleges, community colleges, and similar educational institutions upon payment of annual institutional membership dues. Institutional membership carries no voting nor office-holding privileges, but institutions shall receive *Northwest Science*.
- Sustaining Members: Individual and Organizational Sustaining Membership is available to any individual or organization upon payment of individual or organizational sustaining membership annual dues, respectively. Individual sustaining members have all privileges of members, including voting, office holding and receiving *Northwest Science*. Organizational Sustaining membership carries no voting nor office-holding privileges, but organizations shall receive *Northwest Science*.
- Honorary Life Member: Honorary life membership, granted by the Awards Committee, carries all privileges of membership.

ARTICLE IV
BOARD OF DIRECTORS

Section 1. Purpose, Powers, and Duties. The Board of Directors has the general power to control and manage the affairs, funds, and property of the Corporation in accordance with the fundamental and basic purposes of the Corporation, as expressed in the Articles of Incorporation, dated 7 May 1928.

The Board of Directors may appoint an Executive Director who shall be responsible to the Board for the management of the Corporation. The Board of Directors may further delegate authority to committees or to individual Board Members as it deems necessary for the carrying out of the purposes and business of the Corporation.

Section 2. Number. The number of elected Directors shall be not less than eleven (11), or more than twenty-one (21) members of the Association.

Section 3. Election, Term of Office. Directors shall normally be elected at the annual meeting of the Corporation by a majority vote of the assembled membership. Candidates for board membership shall be nominated for office by a nominating committee. Directors shall be elected to office for a term of three years, or until their successors are duly elected and qualified, except in the case of their earlier death, resignation, or removal from office. A Director may be elected to two consecutive three-year terms. A Director may be re-elected to the Board after a lapse of one year following completion of two consecutive full three-year terms in office. The elected Directors shall be divided into three classes of approximately equal size to provide for the election of approximately one-third of the elected Directors at each annual meeting.

Section 4. Ex Officio Directors, with vote. The officers of the association, the editor of *Northwest Science*, the Program Chair, the immediate past President or the President Elect, plus a representative of the publishing house of its journal, *Northwest Science,* shall serve ex-officio, with all voting rights.

Section 4. Ex Officio Directors, without vote. The Board may also include the President or his/her designee of any auxiliary or adjunct association or group as deemed appropriate by the Directors. Such ex officio Directors will not be voting members of the Board of Directors. Ex officio Directors without vote shall not be counted in determining the presence of a quorum. The Board also may appoint Honorary Directors and/or Directors Emeriti. The terms of such appointments shall be determined by a majority vote of the Directors then serving.

Section 5. Resignation or Removal of Directors. Any Director may resign by giving written notice of his or her resignation to the Board or to the President or Secretary of the Corporation. Such resignation shall take effect at the time specified in such notice and the acceptance of such resignation shall not be necessary to make it effective. Any Director may be removed from office, with or without cause, by a 2/3 majority vote of all Directors then serving in office.

Section 6. Vacancies. Vacancies in the Board, however arising, shall be filled by a majority vote of all Directors then serving in office at any regular meeting of the Board, at a special meeting of the Board called for that purpose, or by appointment by the President of the Board to fill an unexpired term. The person so elected or appointed shall hold office until the next regular meeting of the association, election at which time a member shall be elected to fill the remainder of the unexpired term.

ARTICLE V
MEETINGS

Section 1. Annual Meeting. The annual meeting of the Corporation shall normally be held during the annual scientific meeting each year, or on such other date as may be fixed by the Board of Directors.

Section 2. Regular Meetings, Board. The frequency and dates of regular meetings of the Board of Directors shall be fixed by the Board of Directors, normally at its annual meeting.

Section 3. Special Meetings. Special meetings of the Board of Directors may be called by the President or Vice President of the Board or shall be called by the Secretary at the request in writing of a majority of the voting Directors then serving in office, or by 10 percent of the current members in good standing of the Association.

Section 4. Action Without a Meeting. Action may be taken without a meeting if a consent in writing, setting forth the action so taken, shall be agreed to by a simple majority of the voting Directors then serving in office.

Section 5. Telephone Meetings. Members of the Board or of any committee may participate in person at a Board meeting through use of conference telephone or similar communication equipment, so long as all members participating in such meeting can communicate with one another. Participation in a meeting pursuant to this provision constitutes presence in person at such meeting.

Section 6. Notice of Meetings. Written notice of the time and place of a special meeting of the association shall be sent to each individual member of the association to the last known place of business or residence at least fourteen days, but not more than thirty days prior to the date of such meetings. Notice of regular and special Board meetings shall be sent to each individual Board member to the last known place of business or residence of each individual not less than seven days prior to the date of such meeting or by telephone, or other electronic communications system, not less than five days prior to the date of such meeting. All special Board meeting notices will be accompanied by an agenda.

Section 7. Waiver of Notice. Notwithstanding the provisions of any of the foregoing sections, a meeting of the Board of Directors may be held at such time and place within the western United States and western provinces of Canada as the Board of Directors shall designate, and any action may be taken thereat, if notice thereof is waived in writing by every Director having the right to vote at the meeting.

Section 8. Quorum. Unless provided for differently elsewhere in these By-Laws, a majority of the Directors then serving in office shall constitute a quorum for all meetings of the Association. In the absence of a quorum, a majority of the Directors present may, without giving notice other than announcement at the meeting, adjourn the meeting from time to time until a quorum is obtained. At any such adjourned meeting at which a quorum is present, any business may be transacted which might have been transacted at the meeting as originally called. A meeting at which a quorum is initially present may continue to transact business notwithstanding the withdrawal of Directors if any action taken is approved by at least a majority of the required quorum for such a meeting.

Section 9. Voting. At any meeting of the Directors, every voting Director present in person at such meeting shall be entitled to one vote and, except as otherwise provided by law or by these By-Laws, the act of a majority of the Directors present in person at any meeting at which a quorum is present shall be the act of the Directors.

ARTICLE VI
OFFICERS

Section 1. Principal Officers. The principal officers of the Corporation shall be a President, a Vice President (either the immediate past president or the president elect), a Treasurer, and a Secretary. The President and Vice-President shall be elected to office from among the Directors then serving at the time of the election. The Treasurer and Secretary shall be elected from the membership of the Association. The Board of Directors at any meeting may by resolution elect or appoint additional officers or engage agents and employees and determine their terms of office and compensation, if any, as it may deem advisable.

Section 2. Election and Term of Office. The officers of the Corporation shall normally be elected at the first meeting of a newly constituted Board at which a quorum is present, by a vote of the majority of the Directors present in person at the meeting. The Nominating Committee shall prepare a list of nominations for officer positions, and such list shall be mailed to each Director then serving, along with the notice of said meeting. An officer shall be elected to serve a two-year term and shall hold office until the next annual meeting of the Board following election or until his or her successor shall have been elected, if later, except in the case of death, resignation, or removal as provided for in these By-Laws. No Director may serve in one office for more than two consecutive two-year terms, except for the Secretary and Treasurer which shall have unlimited term limits, unless removed or resigned per Article 4, Section 5, above.

Section 3. Removal of Officers. Any officer may be removed, with or without cause, at any time at any Board meeting at which a quorum is present by a 2/3 vote of the number of Directors then present.

Section 4. Vacancies. Vacancies among the officers, however arising, shall be filled by a majority vote of Directors present at any regular or special meeting of the Board at which a quorum is present. The President has authority to appoint interim officers to serve until the meeting is held at which vacancies are to be filled by majority vote.

Section 5. President. The President shall preside at all meetings of the Board and an Executive Committee, if constituted, and perform all acts incident to the office of President, and shall have such additional powers and duties as may from time to time be assigned to him or her by the Board. Unless otherwise provided for in these By-Laws, the President shall appoint the chairs of each standing committee and may elect to be an ex officio voting member of each Board committee. The President shall sign all contracts and other instruments of writing which shall have been first approved by the Board of Directors.

Section 6. Vice President. In the absence, or inability to act, of the Present, the Vice President shall exercise the powers and perform the duties of President. The Vice President shall also generally assist the President and shall have such other powers and perform such other duties as may from time to time be designated by the President or by the Board of Directors.

Section 7. Treasurer. The Treasurer shall act under the supervision of the Board and shall have charge and custody of, and be responsible for, all the funds of the Corporation and shall keep or cause to be kept, and shall be responsible for the keeping of, accurate and adequate records of the assets, liabilities, and transactions of the Corporation, including filing the appropriate state and federal tax forms required of a 501 (c) (3) corporation. He or she shall deposit, or cause to be deposited, all monies and other valuable effects of the Corporation in the name of and to the credit

of the Corporation in such banks, trust companies, or other depositories as may be designed from time to time by the Board of Directors. He or she shall disburse, or cause to be disbursed, the funds of the Corporation based upon proper vouchers for such disbursement. In general, he or she shall perform all the duties incident to the office of Treasurer and such other duties as may from time to time be assigned to him or her by the President or the Board. The treasurer may empower an Executive Director, if designated, to sign checks with a single signature for expenditures of less than $200.00.

Section 8. Secretary. The Secretary shall keep, or cause to be kept, the minutes of all meetings of the Board and of any meetings of an Executive Committee, and shall see that the minutes of meetings of the Board and of an Executive Committee are distributed promptly to all members of the Board of Directors. He or she shall see that all notices are duly given in accordance with these By-Laws and as required by law. He or she shall be custodian of the seal of the Corporation and shall affix and attest the seal to any and all documents the execution of which on behalf of the Corporation under its seal shall have been specially or generally authorized by the Board of Directors. He or she shall have charge of the books, records, and papers of the Corporation relating to its organization as a corporation and shall see that all reports, statements, and other documents required by law are properly kept or filed, except to the extent that the same are to be kept or filed by the Treasurer. In general, he or she shall perform all duties incident to the office of Secretary and such other duties as may from time to time be assigned to him or her by the President or by the Board of Directors.

Section 9. Bonding. Any officer or employee of the corporation shall, if required by the Board of Directors, give such security for the faithful performance of his or her duties as the Board of Directors may require. The cost of bonding shall be paid by the Corporation should it be required.

ARTICLE VII
COMMITTEES

Section I. The Board of Directors may by resolution at any meeting of the Board designate standing, ad hoc, and/or special committees of the Board. The Board may appoint an Advisory Council and/or honorary groups. The terms of appointment and expectations of service of any advisory or honorary group shall be determined by the Board of Directors.

Section 2. Membership. Normally, the President of the Board of Directors shall appoint the chair of each Board committee. Normally, the Chair of each committee shall appoint the other committee members in consultation with the President of the Board. Each committee normally shall consist of at least three members, at least one of whom shall be a voting member of the Board of Directors. Unless otherwise provided for in these By-Laws, any committee designated by the Board of Directors may include as full voting members of such committees such persons, whether or not Directors or Officers of the Corporation, as the Board of Directors shall determine. Each such committee shall have power to the extent delegated to it by the Board of Directors and in accordance with federal nonprofit law. Each committee shall keep minutes of proceedings and report to the Board of Directors.

Section 3. Executive Committee. The Executive Committee shall include in its membership the current officers of the Corporation. The President of the Board shall serve as Chair. The Executive Committee may, during intervals between meetings of the Board, exercise all the powers of the

Board in the management of the business and affairs of the Corporation, except as otherwise provided by law, these By-Laws, or by resolution of the Board. The presence of a majority of the members of the Executive Committee then serving in office shall be necessary and sufficient to constitute a quorum and the act of a majority of the members of the Executive Committee present at a meeting of the Committee at which a quorum is present shall be the act of the Committee. The Executive Committee shall keep full and fair records and accounts of its actions which shall be presented at the next meeting of the Board of Directors for ratification by majority vote. Minutes of the Executive Committee shall be distributed to all members of the Board of Directors.

Section 4. Committee Meetings. Unless otherwise provided for in these By-Laws, a majority of the members then serving on a Committee constitutes a quorum for the meeting of the Committee and the vote of a simple majority of those present at a meeting at which a quorum is present, constitutes an action of the Committee.

Section 5. Standing Committees. Standing committees of the Association shall include, but not be limited to, the following:

- Nominating Committee. Consisting of three (3) members, at least one of which is a member of the Board of Directors and appointed by the President, to act as the nominating committee for officers and trustees of the Association, the names of which are to be presented at the annual business meeting for majority vote.
- Student Grants Committee. This Committee shall consist of three (3) members, at least one of which is a member of the Board of Directors and appointed by the President. This committee shall consider requests for grants from the Student Research Fund and recommend candidates for grants to the Board of Directors.
- Awards and Honors Committee. This committee shall consist of three (3) members, at least one of which is a member of the Board of Directors and appointed by the President. This Committee may recommend candidates for special honors and awards to the Board of Directors.
- Program Committee. This committee shall consist of a minimum of two (2) members, at least one of which is a member of the Board of Directors and appointed by the President, whose primary purpose is to assist the individual responsible for organizing the annual association meeting.

ARTICLE VIII
INDEMNIFICATION

Every person who is or shall be a Director or Officer of the Corporation and his or her personal representatives will be indemnified by the Corporation against all costs and expenses reasonably incurred by or imposed upon him or her in connection with or resulting from any action, suit, or proceeding to which he or she may be made a party by reason of his or her being or having been a Director or Officer of the Corporation or of any subsidiary or affiliate thereof, except in relation to such matters as to which he or she shall finally be adjudicated in such action, suit, or proceeding to have acted in bad faith and to have been liable by reason of willful misconduct or willful negligence in the performance of his or her duty as Director or Officer. Costs and expenses of actions for which this Article provides indemnification shall include among other things, attorneys' fees, damages, and reasonable amounts paid in settlement. The Board will secure and maintain Directors, Officers, and Trustees Liability Insurance.

ARTICLE IX
MISCELLANEOUS

Section 1. Personal Liability. No Director shall be held personally liable for any debts of the Corporation.

Section 2. Fiscal Year. The fiscal year of the Corporation shall be January 1 to December 30.

Section 3. Contracts, Checks, Bank Accounts, Etc. The Board of Directors is authorized to select such banks or depositories as it shall deem proper for the funds of the Corporation. The Board shall determine who, if anyone, in addition to the President and the Treasurer, shall be authorized from time to time on the Corporation's behalf to sign checks, drafts, or other orders for the payment of money, acceptances, notes, or other evidences of indebtedness, to enter into contracts or to execute and deliver other documents and instruments.

Section 4. Corporate Seal. The seal of the Corporation shall be circular in form and shall bear the name of the Corporation, and the year of incorporation.

Section 5. Loans. This corporation shall not make any loan of money or property to or guarantee the obligation of any Director, Officer, or Employee. Provided, however, that this corporation may advance money to a Director, Officer or Employee of this corporation or any subsidiary for expenses reasonably anticipated to be incurred in the performance of duties of such Director, Officer, or Employee so long as such individual would be entitled to be reimbursed for such expenses that advance.

ARTICLE X
AMENDMENTS

These By-Laws may be altered, amended, or repealed in whole or in part at any duly organized meeting of the Association, by a two-thirds majority vote of the voting members. Any proposal to amend these By-Laws shall be included with the notice of the meeting at which the amendment is proposed.

ARTICLE XI
DISTRIBUTION ON DISSOLUTION

Upon dissolution of the Corporation, the Board of Directors shall, after paying or making provision for the payment of all liabilities of the Corporation, distribute all the assets of the association consistent with the purposes of the Corporation to such organization or organizations as shall at the time qualify as exempt organizations under Section 501(c)(3) of the Internal Revenue Code of 1986, as amended from time to time, in such manner as the Board of Directors shall determine. Any such assets not so distributed shall be distributed by the district court of the county in which the principal office of the Corporation is then located, exclusively for such purposes or to such organizations, as such court shall determine to be consistent with the support of scientific excellence within western North America. At the date of development of these bylaws, the Board designates the American Association for the Advancement of Science as the recipient with the instruction that the transferred corpus should be used to support scientific research of students through the development of a permanent endowment trust fund.

A signature page listing all Board Members at the ratification of these By-laws will follow.

Michael J. Wisdom, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850 mwisdom@fs.fed.us

Barbara C. Wales, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850

Richard S. Holthausen, USDA Forest Service, 2500 S. Pine Knoll, Flagstaff, Arizona 86001

Wendel J. Hann, USDA Forest Service, 2015 Poplar, Leadville, Colorado 80461

Miles A. Hemstrom, USDA Forest Service, Pacific Northwest Research Station, P.O. Box 3623, Portland, Oregon 97208

and

Mary M. Rowland, USDI Bureau of Land Management, 1401 Gekeler Lane, La Grande, Oregon 97850

A Habitat Network for Terrestrial Wildlife in the Interior Columbia Basin

Abstract

Habitat managers need information about landscape conditions in relation to the composite requirements of species that deserve attention in conservation planning. Consequently, we characterized and mapped a broad-scale network of habitats for five suites of terrestrial vertebrates in the 58 million-ha Interior Columbia Basin (Basin). These five suites, referred to as Families, are composed of 44 species whose habitats have declined strongly from historical (circa 1850-1890) to current periods in the Basin, and thus are of conservation focus. Two of the five Families consist of species that depend on old forests. Species in another Family depend on early-seral forests. Species in the remaining Families depend on sagebrush-steppe or open canopy sagebrush and grasslands. For each Family, we characterized current habitat conditions at the scale of the watershed (mean size of 22,500 ha). Each watershed was classified as one of three conditions. Watersheds in Condition 1 contained habitats whose quality or abundance have changed little since the historical period. By contrast, watersheds in Condition 2 or 3 contained habitats that have changed from historical conditions, but in different ways. Watersheds in Condition 2 had habitats of high abundance but moderate resiliency and quality, whereas watersheds in Condition 3 contained habitats of low abundance or low resiliency and quality. The majority of watersheds (59%-80%) were in Condition 3 for all five Families, whereas the lowest percentage (5%-25%) of watersheds was in Condition 2 for four of five Families. Connectivity among watersheds for all Families appeared low in many parts of the Basin due to spatial gaps associated with areas of habitat extirpation. Our condition maps constitute a broad-scale network of habitats that could be useful for developing multi-species research hypotheses and management strategies for the Basin.

Introduction

Habitats for a myriad of terrestrial vertebrates are declining across the world. Causes for decline are many and varied. Intensive timber harvest, extensive mining, excessive livestock grazing, conversion of habitats to urban and agricultural uses, recreational activities, road access, and widespread invasion of exotic flora and fauna are major causes of decline (Western and Pearl 1989, Noss and Cooperrider 1994). As a result, habitat loss is a major problem for many terrestrial vertebrates. Decline has been especially notable for old-forest, shrub-steppe, grassland, riparian, and wetland habitats (Noss et al. 1995).

In response to these problems, efforts to assess and manage habitats have focused increasingly on large areas, multiple species, and integration of a suite of beneficial management strategies. For example, The Nature Conservancy has completed over 50 Rapid Ecological Assessments (REAs) since 1991, with each assessment encompassing millions of hectares, hundreds or thousands of plant and animal species, and major biomes containing the world's highest biodiversity (Sayre et al. 2000). Results from REAs now form the basis for broad-scale conservation strategies of The Nature Conservancy across the world.

REAs and similar broad-scale assessments, such as GAP analysis (Scott et al. 1993), are coarse-filter approaches on which habitat management can be based. Coarse-filter approaches assume that conserving representative land areas and habitats over large areas will provide for the needs of all associated species, communities, and ecological processes (Noss 1987, Hunter 1991). By contrast,

fine-filter approaches provide specific habitats for single or few species (Marcot et al. 1994).

Theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969), which led to modern-day principles of conservation biology (Soulé 1986, Noss and Cooperrider 1994) and landscape ecology (Forman and Godron 1987), have direct implications for the design of coarse-filter approaches. That is, coarse-filter approaches must provide habitats of sufficient size, connectivity, quality, and resiliency to withstand the deleterious effects of environmental variation, changing climate, disturbance regime dynamics, demographic stochasticity, inbreeding depression, and Allee effects, all of which contribute to extinction of small or isolated populations (Burgman et al. 1993). If habitats are small, degraded, not connected, or cannot be sustained, the probability of population extinction for species that depend on such habitats increases dramatically (Doak and Mills 1994, Harrison and Fahrig 1995). Moreover, coarse-filter approaches require consideration of habitat needs for a comprehensive set of species associated with environments that have declined or have been degraded (Hunter 1991).

In accordance with these principles, Wisdom et al. (2000) conducted a coarse-filter assessment of 91 species of terrestrial vertebrates in the Interior Columbia Basin (Basin). The 91 species were associated with upland environments and were selected because of empirical evidence of habitat or population decline. Moreover, habitats for these upland species could be mapped accurately with the large pixel size of 1 km^2 that was available for coarse-filter assessment across the vast area of the 58 million-ha Basin.

As part of their coarse-filter assessment, Wisdom et al. (2000) placed the 91 upland species into 40 groups, and subsequently placed 37 of the groups into 12 Families, using a hierarchical classification system based on similarities in habitat requirements. (Note that the term "Families" has no taxonomic meaning, but instead identifies robust similarities in habitat requirements among large groups of species, regardless of taxonomic relation.) Habitat trends for each of the 91 species, 40 groups, and 12 Families were assessed at multiple spatial scales, using habitat estimates for historical (circa 1850-1890) and current periods. Hann et al. (1997) and Wisdom et al. (2000) described the innovative methods by which historical and current conditions were estimated in the Basin, and documented the accuracy and sources of uncertainty associated with these methods.

In this paper, we build on the results of Wisdom et al. (2000) to further evaluate habitat conditions for 44 of the 91 upland terrestrial vertebrates in the Basin. We provide rationale for selection of the 44 species, characterize habitat conditions for these species using a coarse-filter approach, and describe the results in relation to relevant theory and implications for management. Within this framework, our goal was to characterize areas for the 44 species where (1) habitats have changed little in quality or abundance from historical conditions; (2) habitats have changed from historical conditions and are of high abundance but of moderate quality and resiliency; and (3) habitats have changed from historical conditions and are of low abundance or low quality and resiliency. These three characterizations constitute a coarse-filter network that could be useful for developing multi-species research hypotheses and management strategies in the Basin. These potential benefits were the primary motivations for our analysis.

Our work was conducted as part of the Interior Columbia Basin Ecosystem Management Project (ICBEMP). The ICBEMP was established in January 1994 through a charter signed by the Chief of the USDA Forest Service (FS) and the Director of the USDI Bureau of Land Management (BLM) (USDA Forest Service 1996). The charter directed that work be undertaken to develop and adopt an ecosystem-based strategy for lands administered by the FS and BLM (FS-BLM) within the Basin. The Science Assessment Area of ICBEMP extends over 58 million ha in Washington, Oregon, Idaho, Montana, and small portions of Wyoming, Nevada, and Utah (Figure 1). Fifty-three percent of the Basin is public land administered by FS-BLM, which was the focus of the ICBEMP.

Study Area

The ICBEMP Science Assessment Area includes all areas drained by the Columbia River within the United States that are east of the crest of the Cascade Range; also included are portions of the Klamath and Great Basins in Oregon (Figure 1).

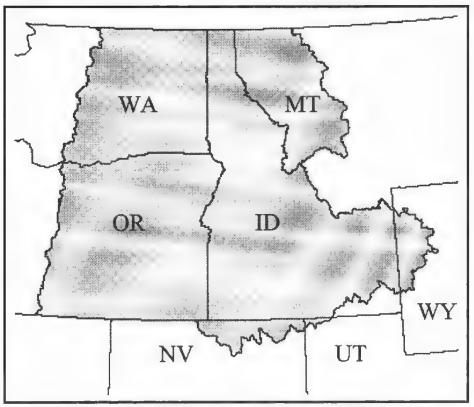

Figure 1. Boundaries of the science assessment area for the Interior Columbia Basin Ecosystem Management Project in the western United States. The science assessment area includes eastern Washington (WA), eastern Oregon (OR), northwest Montana (MT), most of Idaho (ID), and small portions of northwest Wyoming (WY), northwest Utah (UT), and northern Nevada (NV).

The 58 million-ha Basin is subdivided into four spatial scales (Gravenmier et al. 1997): (1) Ecological reporting unit (ERU), (2) subbasin, (3) watershed, and (4) subwatershed. Ecological reporting units, of which there are 13, range in size from about 740,000 to 6,800,000 ha (mean size of approximately 2,375,000 ha). The 164 subbasins average about 345,000 ha, whereas the 2,562 watersheds average about 22,500 ha each. The 7,654 subwatersheds average about 7,700 ha. Quigley et al. (1996) described these spatial scales and the diverse ecological components of the Basin in detail. Marcot et al. (1997), Lee et al. (1997), and Raphael et al. (1998) further described flora and fauna occurring in the Basin.

Methods

Selecting Groups of Species for Analysis

We selected 44 species included in 5 of the 12 Families from Wisdom et al. (2000) for our analysis (Table 1). The five Families included species that depend on low-elevation, old-forest (Family 1), old-forest encompassing a broad range of elevations (Family 2), low-elevation, early-seral forest (Family 4), sagebrush (Family 11), and open-canopy shrubland and grassland (Family 12). We selected species in these five Families because (1) their habitats have undergone extensive decline or their ranges have contracted substantially since the historical period; (2) their habitats also encompass habitats in decline for species in other Families that were not selected; and (3) their habitat requirements typically are more stringent than species in other Families.

Notably, we did not select species of wide-ranging mammals such as grizzly bear (*Ursus arctos*), gray wolf (*Canis lupus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). These species are affected strongly by human disturbances, have large home ranges, and require different scales and environmental conditions for conservation planning than do species in the five Families that we analyzed (Raphael et al. 2001). Similarly, we did not select the 82 species associated with riparian, wetland, and other linear or fine-scale features that were identified by Wisdom et al. (2000) as deserving conservation attention in the Basin. Habitats for these species could not be analyzed in a coarse-filter assessment because such fine-scale habitats cannot be mapped accurately with a pixel size of 1 km^2. Consequently, we assume that different approaches than those used here are needed to characterize environmental conditions for the wide-ranging mammals and the riparian and wetland species identified by Wisdom et al. (2000).

Characterizing Habitat Conditions

Goals and Assumptions

Our goal was to characterize broad-scale conditions that reflected composite differences in the quantity, quality, resiliency, and connectivity of habitats for the 44 vertebrates species of conservation concern that composed Families 1, 2, 4, 11, and 12 (Table 1). A second goal was to focus our characterization in areas containing public lands to facilitate conservation planning on and near such lands. We assumed that our broad-scale conditions could serve as a composite, coarse-filter approximation from which conservation planning could be done over millions of hectares of the Basin in an efficient and effective manner for all 44 species, and for vertebrates in the other Families whose habitats in decline overlap those of the 44. Moreover, we assumed that our

TABLE 1. Common and scientific names of 44 vertebrate species of conservation focus that were selected from Wisdom et al. (2000) for characterization of habitat conditions, and the group and family in which Wisdom et al. placed each species as part of their multi-species assessment.

Family	Group	Common name (*scientific name*)
1. Old forest, low elevation[1]	1	White-headed woodpecker (*Picoides albolarvatus*)
	1	White-breasted nuthatch (*Sitta carolinensis*)
	1	Pygmy nuthatch (*Sitta pygmaea*)
	2	Lewis' woodpecker (*Melanerpes lewis*)
	3	Western gray squirrel (*Sciurus griseus*)
2. Old forest, all elevations[2]	4	Blue grouse (*Dendrogapus obscurus*)
	5	Northern goshawk (*Accipiter gentiles*)
	5	Flammulated owl (*Otus flammeolus*)
	5	American marten (*Martes americana*)
	5	Fisher (*Martes pennanti*)
	6	Vaux's swift (*Chaetura vauxi*)
	6	Williamson's sapsucker (*Sphyrapicus thyroideus*)
	6	Pileated woodpecker (*Dryocopus pileatus*)
	6	Hammond's flycatcher (*Empidonax hammondii*)
	6	Chestnut-backed chickadee (*Poecile rufescens*)
	6	Brown creeper (*Certhia americana*)
	6	Winter wren (*Troglodytes troglodytes*)
	6	Golden-crowned kinglet (*Regulus satrapa*)
	6	Varied thrush (*Ixoreus naevius*)
	6	Silver-haired bat (*Lasionycteris noctivagans*)
	6	Hoary bat (*Lasiurus cinereus*)
	7	Boreal owl (*Aegolius funereus*)
	8	Great gray owl (*Strix nebulosa*)
	9	Black-backed woodpecker (*Picoides arcticus*)
	10	Olive-sided flycatcher (*Contopus borealis*)
	11	Three-toed woodpecker (*Picoides tridactylus*)
	11	White-winged crossbill (*Loxia leucoptera*)
	12	Woodland caribou (*Rangifer tarandus caribou*)
	13	Northern flying squirrel (*Glaucomys sabrinus*)
4. Forest stand initiation[3]	18	Lazuli bunting (*Passerina amoena*)
11. Sagebrush[4]	33	Greater Sage-grouse (*Centrocercus urophasianus*)
	33	Sage thrasher (*Oreoscoptes montanus*)
	33	Brewer's sparrow (*Spizella breweri*)
	33	Sage sparrow (*Amphispiza belli*)
	33	Lark bunting (*Calamospiza melanocorys*)
	33	Pygmy rabbit (*Brachylagus idahoensis*)
	33	Sagebrush vole (*Lemmiscus curtatus*)
	34	Black-throated sparrow (*Amphispiza bilineata*)
	34	Kit fox (*Vulpes velox*)
	35	Loggerhead shrike (*Lanius ludovicianus*)
12. Grassland, open sagebrush[5]	36	Col. sharp-tailed grouse (*Tympanuchus phasianellus columbianus*)
	37	Clay-colored sparrow (*Spizella pallida*)
	37	Grasshopper sparrow (*Ammodramus savannarum*)
	37	Idaho ground squirrel (*Spermophilus brunneus*)

[1] Habitats consist primarily of lower montane forests in late-seral condition.
[2] Habitats consist primarily of montane to subalpine forests in late-seral condition.
[3] Habitats consist primarily of lower montane and montane forests in early-seral condition.
[4] Habitats consist primarily of sagebrush communities.
[5] Habitats consist primarily of bunchgrass communities as well as sagebrush and other shrubland communities with open canopies.

characterization of broad-scale conditions could be used for large-scale, long-term conservation planning but would require augmentation at local scales, using fine-scale data on individual species or groups, to ensure appropriate management implementation. Finally, we assumed that our characterization followed principles of conservation biology, in that suitable habitats are identified in terms of composition and structure (as defined by Wisdom et al. 2000), size (as indexed by estimates of habitat abundance), quality and resiliency (as indexed by a disturbance departure variable), and connectivity (as indexed by mapping of spatial gaps), described below.

Habitat Abundance

We used estimates of the number of hectares of habitat from Wisdom et al. (2000) for the 19 groups of the 44 species within Families 1, 2, 4, 11, and 12 (Table 1) to establish three classes of habitat abundance among watersheds for each Family. First, we calculated the mean number of hectares of habitat currently present in each watershed among all groups of species in a Family. Second, for each Family, we ranked the watersheds from highest to lowest, based on the mean number of hectares in each watershed. Finally, we placed the ranked watersheds in three classes: Class A, defined as watersheds with a ranking in the top two quartiles of all watersheds for a Family; Class B, composed of watersheds in the next-lowest quartile for a Family; and Class C, made up of watersheds in the lowest quartile. These three classes represent a ranking of watersheds at three levels of habitat abundance: high (Class A); low-moderate (Class B); and very low (Class C).

Habitat Quality and Resiliency

We combined the three classes of habitat abundance with a variable that reflected habitat quality and resiliency to express the composite quantity, quality, and resiliency of habitat in each watershed for each Family. To estimate quality and resiliency, we used the disturbance departure variable derived by Hann et al. (2002). This variable is a composite estimate of departure from the historical landscape mosaic and succession-disturbance regimes, caused by the cumulative effects of past timber management, excessive livestock grazing, wildfire suppression, road development, agricultural conversions, invasions of exotic plants, and other human activities that do not mimic historical regimes (Hann et al. 2002). Levels of disturbance departure reflect the degree of coarse-scale change in patch size, composition, and arrangement; frequency and intensity of fire events; timing and severity of tree mortality associated with insect defoliation and pathogen events; successional rates and pathways; timing and intensity of ungulate grazing; composition of native versus non-native vegetation; and human activities and presence. The reader is referred to Hann et al. (2002) for details on the spatial assignment of the disturbance departure variable to watersheds.

Disturbance departure was derived as four classes (low, moderate, high, very high), with very high representing the greatest level of deviation from historical conditions (Hann et al. 2002). A departure class was assigned to each watershed, based on the combination of three broad-scale variables previously developed by Hann et al. (1997): landscape pattern, potential vegetation group, and succession-disturbance regime. Hann et al. (2002) used these three variables to derive the disturbance departure variable, based on their ability to reflect the mid- and fine-scale data concerning change in landscape mosaic and succession-disturbance regimes. Data for these variables are from Hessburg et al. (1999), based on photo-interpreted maps and change in fine-scale features estimated from sample plots.

The disturbance departure variable indexes habitat quality because within-stand composition and structure of vegetation, and among-stand spatial arrangement and pattern of vegetation, are highly correlated with the variables that compose the departure variable. For example, densities of large snags and large logs in forest stands decline with increasing road density, timber harvest, and wildfire suppression (Hann et al. 1997), all of which are correlated with increasing levels of disturbance departure (Hann et al. 2002).

The disturbance departure variable also indexes resiliency because the rate of habitat recovery and the return of desired habitat functions, following disturbance events, are highly correlated with variables that compose the departure variable. For example, resiliency of native vegetation in rangelands is increasingly disrupted by invasion of exotic plants, increasing road density, higher frequency and intensity of wildfire events, and excessive

livestock grazing. All of these factors are correlated with increasing levels of disturbance departure (Hann et al. 2002).

We define resiliency as the capability of system biota and their environments to renew the cycle of functions, processes, and conditions following disturbance, as defined by Hann et al. (1997) from concepts and interpretations of Allen and Hoekstra (1992) and the summary by Noss (2001). Under this definition, habitats of high resiliency have a high probability of maintenance and recovery under disturbance regimes of fire, disease, herbivory, and insect defoliation (Hann et al. 1997, Hann et al. 2002). Use of this definition implies that habitat quality and resiliency are highly correlated. That is, habitats that are not resilient cannot maintain quality over extended time periods.

While our definition of resiliency is compatible with our goal to characterize habitats for broad-scale, long-term conservation planning, habitats that are not resilient also could be important. The long-term contribution of non-resilient habitats, however, would be negligible. Consequently, identification of high-quality but non-resilient habitats requires examination at local scales, using fine-scale data, to ensure appropriate consideration of these habitats over short time periods in relation to our broad-scale characterization of conditions that was designed for long-term planning.

Habitat Conditions

We used the following rules to combine the four classes of disturbance departure with the three classes of habitat abundance to estimate three habitat conditions for each Family during the current period. Condition 1 was defined as any watershed with low disturbance departure, regardless of habitat abundance (class A, B, or C); this condition reflects high resiliency of habitat and a quantity and quality of habitat that is relatively unchanged from historical conditions. Condition 2 was defined as any watershed with moderate disturbance departure and habitat abundance in class A (watersheds within the two highest quartiles of habitat abundance); this condition reflects moderate resiliency, moderate quality, and high quantity of habitat. Condition 3 was defined as any watershed that did not qualify as Condition 1 or 2. Accordingly, Condition 3 occurred in watersheds within the two lowest quartiles of habitat abundance (Class B or C) that had a disturbance departure other than low, or in watersheds with habitat abundance of Class A that had a disturbance departure of high or very high; this condition typically reflects habitats of low quantity or low resiliency and quality.

Condition 1 can be thought of as watersheds with habitats similar to historical conditions, while Condition 2 might be considered watersheds with degraded but abundant habitats. By contrast, Condition 3 could be described as watersheds with degraded and uncommon, rare, or extirpated habitats.

We applied our rule set to any watershed, for a given Family, that was within the range of any species in the Family, and that contained habitat for the Family during the historical or current periods. Estimates of species ranges, and of habitat occurrence during historical and current periods, were obtained from Wisdom et al. (2000). Applying our rule set to watersheds that contained habitat for a Family during the historical period was important because many of these watersheds no longer support habitat. This loss of habitat over time would otherwise have been overlooked, thus biasing our evaluation.

While our rule set may appear to combine too many different characteristics in too few categories of habitat condition, we explored a variety of alternative rules for combining the classes of disturbance departure and habitat abundance. We concluded from these explorations that the three habitat conditions were efficient at providing a coarse-filter approximation of the composite differences in habitat quantity, quality, and resiliency for each Family, in accordance with our goals and assumptions. For example, we found that watersheds in Condition 3 typically contained habitats of very low abundance, with a high or very high departure that indicated low or very low quality and resiliency. We also found that habitats had been extirpated in many Condition 3 watersheds, an occurrence unique to this Condition. These characteristics of Condition 3 contrasted strongly with those of Conditions 1 and 2.

Condition Analysis

Use of our rule set resulted in classification of three mutually exclusive habitat conditions among watersheds within the range of species in each Family. Accordingly, we used the rule set to map watersheds in each of the three habitat conditions

for each Family during the current time period. We also calculated the percentage of watersheds in each habitat condition. Finally, we calculated the percent overlap of watersheds in each habitat condition, and all conditions combined, with wilderness areas, roadless areas, and National Parks; this was done to gain insight about the relation between habitat conditions and areas where custodial (non-active) management is a common practice (with the exception of fire suppression, which has occurred in many of these areas [Hann et al. 1997]).

We did not apply the rule set to the small percentage of watersheds (18%) composed entirely of private lands. We excluded such watersheds because (1) our analysis was designed to characterize conditions on public lands, particularly for FS-BLM management; and (2) managers of public lands have no jurisdiction or control over private lands. Private lands, however, are intermixed with public lands in most watersheds that we analyzed, and in these cases, coordination between public and private landowners is more likely to occur. We therefore included all watersheds that contained any amount of public ownership in our analysis. Public lands included all local, state, and federal ownerships; that is, all lands not privately owned.

Identifying Gaps in Connectivity

Although we did not conduct a formal evaluation of habitat connectivity within or across watersheds, we identified the watersheds for each Family that historically contained habitat, but where habitat currently is extirpated or rare, as defined below. Estimates of historical and current occurrence of habitats were obtained from Wisdom et al. (2000).

Watersheds with extirpated habitats were defined as those historically containing habitat but no habitat currently for each Family. Watersheds with rare habitats were defined as those with percent area of habitat >0% but <1% for a Family. By mapping and enumerating these watersheds, we could quantify and examine spatial gaps across watersheds where habitats for each Family were absent or nearly absent, but were present historically. We chose to map watersheds with extirpated habitats, and those where habitats were rare, after examining a frequency distribution of habitat area for all watersheds for each Family. This examination revealed a relatively large set of watersheds with little or no habitat for the current time period that historically contained larger amounts of habitat. Consequently, this mapping exercise was intended to reveal spatial gaps in connectivity that could be addressed through habitat restoration, because such watersheds historically supported a larger amount of habitat for each Family.

Importantly, our estimates of extirpated and rare habitats, as with all our habitat estimates, were based on the large pixel size of 1 km^2 that was used as our mapping unit. With this pixel size, cover types that occur in small patches of <4 ha often are not mapped, unless such patches compose >25% of a given pixel (>25 ha) (Wisdom et al. 2000). Consequently, relatively small, isolated patches of habitat could still be present in watersheds that we defined as extirpated or rare.

Results

All five Families had the highest percentage of watersheds in Condition 3, which indexed areas of degraded and uncommon, rare, or extirpated habitats (Table 2). Watersheds in Condition 2, which indexed areas of degraded but abundant habitats, composed the lowest percentage of watersheds for four of the five Families (Families 1, 2, 4, and 12, Table 2). Family 11 had the lowest percentage of watersheds in Condition 1, which indexed areas with habitats similar to historical conditions.

Watersheds in Condition 1 had 64%-84% overlap with wilderness areas, roadless areas, or National Parks for all five Families (Table 2). By contrast, watersheds in Conditions 2 and 3 had 7%-23% overlap with these areas. Condition 1 was particularly concentrated in parts of northwest Montana, central Idaho, northeast Oregon, the Cascade Mountains of Washington, southeast Oregon, southwest Idaho, and northwest Wyoming (Figures 2-6). Watersheds in Condition 3 were found across large areas of the Basin, with geographic concentrations varying by Family (Figures 2-6). Watersheds in Condition 2 also varied geographically by Family.

Family 1 (low-elevation, old forest) had a particularly low percentage of watersheds in Condition 1 and high percentage in Condition 3 (Table 2). Watersheds in Condition 3 for this Family were widespread (Figure 2). Notably, watersheds where habitats were extirpated composed 30% of all

TABLE 2. Percentage (number) of watersheds by habitat condition and containing extirpated habitats, rare habitats, and wilderness areas, roadless areas, or National Parks, for five Families of 44 vertebrates species of conservation focus in the Interior Columbia Basin. Habitat conditions and extirpated and rare habitats are defined in the methods.

		Percentage (Number) of Watersheds			
Family	Habitat Condition	By Habitat Condition	With Extirpated Habitats	With Rare Habitats	With Wilderness Roadless Areas or National Parks
1	1	14 (176)	0 (0)	4 (51)	81
	2	6 (73)	0 (0)	0 (0)	7
	3	80 (999)	37 (373)	11 (142)	22
	All	100 (1248)	30 (373)	15 (192)	29
2	1	22 (313)	0 (0)	<1 (4)	84
	2	10 (148)	0 (0)	0 (0)	13
	3	68 (998)	3 (28)	7 (98)	18
	All	100 (1459)	2 (28)	7 (102)	29
4	1	22 (293)	0 (0)	<1 (7)	77
	2	5 (62)	0 (0)	0 (0)	23
	3	73 (955)	35 (333)	6 (75)	17
	All	100 (1310)	25 (333)	6 (82)	30
11	1	15 (189)	0 (0)	<1 (10)	66
	2	25 (310)	0 (0)	0 (0)	20
	3	59 (730)	25 (179)	5 (56)	21
	All	100 (1229)	15 (170)	5 (66)	26
12	1	18 (235)	0 (0)	<1 (6)	64
	2	13 (165)	0 (0)	0 (0)	20
	3	69 (897)	19 (171)	3 (42)	18
	All	100 (1297)	13 (171)	4 (48)	27

watersheds, and all extirpated habitats were associated with Condition 3 (Table 2). Watersheds characterized by rare habitats composed an additional 15% of all watersheds. Watersheds with extirpated and rare habitats for Family 1 occurred mostly in northern parts of the Basin (Figure 2). By contrast, most watersheds in Condition 2 for Family 1 occurred in southwestern areas.

Family 2 (broad elevation, old forest) had a larger percentage of watersheds in Condition 1 than did Family 1, and a smaller percentage in Condition 3 (Table 2). Most watersheds, however, were still characterized as Condition 3, but the percentage of watersheds where habitat was extirpated or rare was lowest of all Families (Table 2). Most watersheds in Condition 2 for this Family occurred in the southwestern parts of the Basin, whereas distribution of watersheds in Condition 3 was widespread (Figure 3).

Family 4 (early-seral forest) had a particularly high percentage of watersheds in Conditions 1 and 3 (Table 2). Extirpated habitats occurred in 25% of all watersheds, and rare habitats occurred in an additional 6% of watersheds (Table 2). Watersheds in Condition 3 were found throughout the Basin for Family 4, with extirpated and rare habitats concentrated in southwestern and northeastern areas (Figure 4). Watersheds in Condition 2 were largely absent in Oregon and scattered throughout other areas for this Family (Figure 4).

Families 11 (sagebrush) and 12 (open-canopy sagebrush and grassland) had a majority of watersheds in Condition 3 and a low percentage in Condition 1 (Table 2). Extirpated or rare habitats for these Families occurred in 17%-20% of watersheds (Table 2) and were widespread, with the exception of southeast Oregon, where Condition 2 was dominant (Figures 5, 6).

Discussion

Network Characteristics and Patterns

Our results depict broad-scale patterns of habitat conditions for the five Families in the Basin. One important pattern is the high overlap of Condition 1 watersheds with high-elevation wilderness areas, roadless areas, or National Parks for all five Families. Moreover, Condition 1 watersheds compose only 14%-22% of all watersheds among the Families. In combination, these results demonstrate

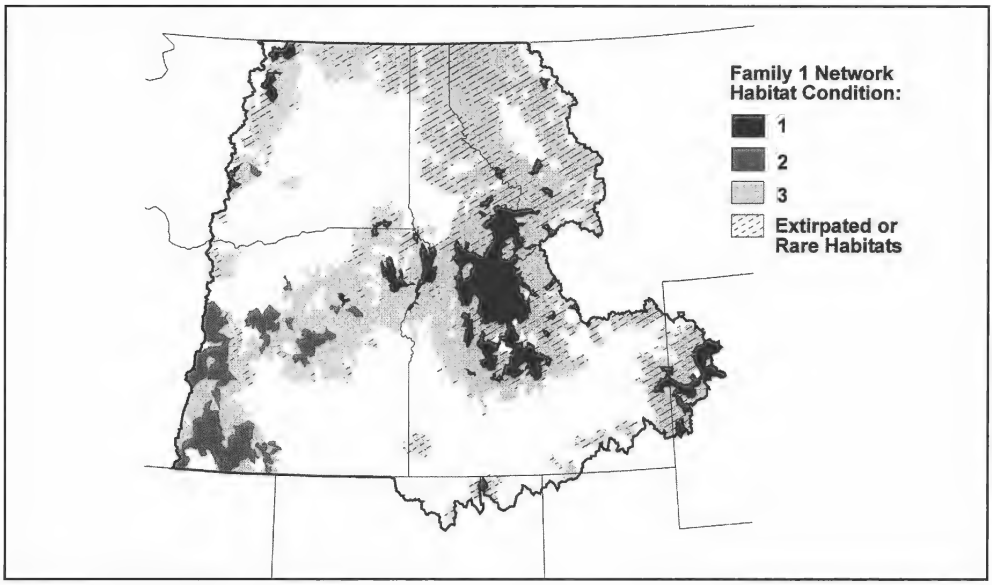

Figure 2. Network for Family 1, composed of low-elevation, old-forest habitats. Watersheds in Condition 1 contain habitats that have undergone little change since the historical period. Watersheds in Condition 2 or 3 have changed since the historical period, but in different ways. Watersheds in Condition 2 are characterized by habitats of high abundance but moderate resiliency and quality. Watersheds in Condition 3 contain habitats of low abundance or low resiliency and quality. Watersheds with extirpated habitats are those containing habitat historically but no habitat currently. Watersheds with rare habitats are those containing >0% but <1% of habitat area for the Family. White areas are watersheds that either contain no public lands or are outside the range of species in the Family.

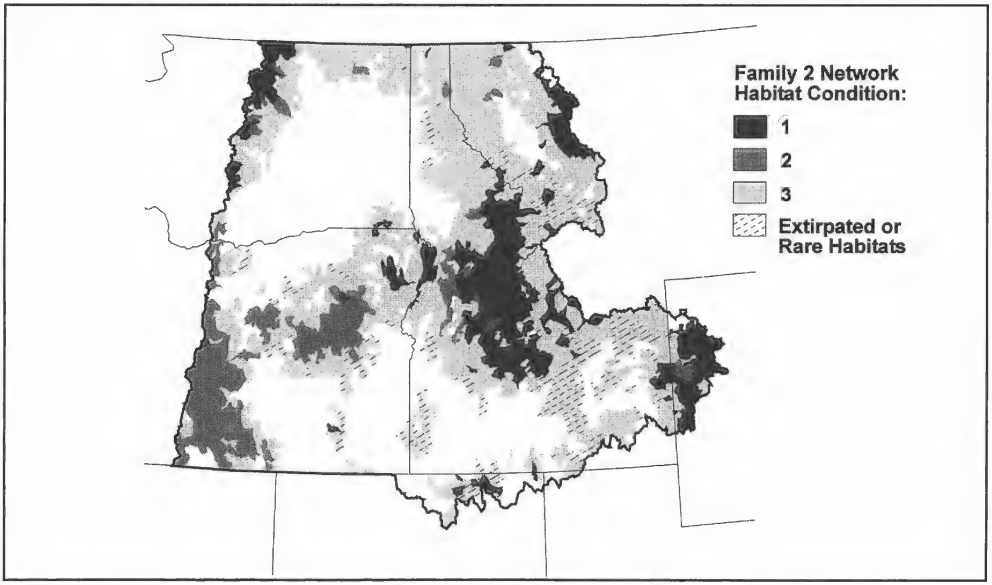

Figure 3. Network for Family 2, composed of broad-elevation, old-forest habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

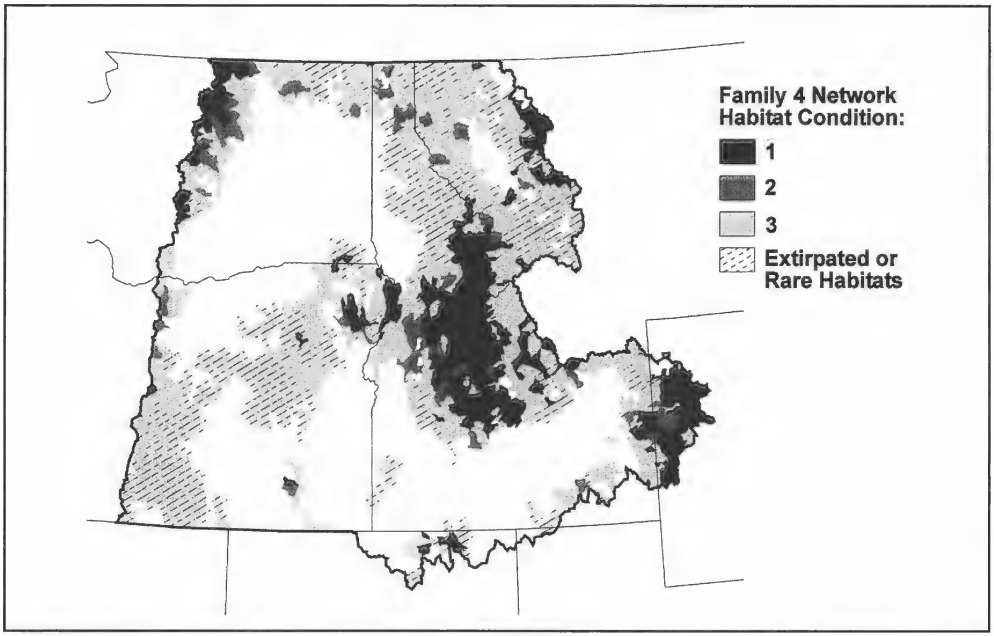

Figure 4. Network for Family 4, composed of habitats of lower montane and montane early-seral forest. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

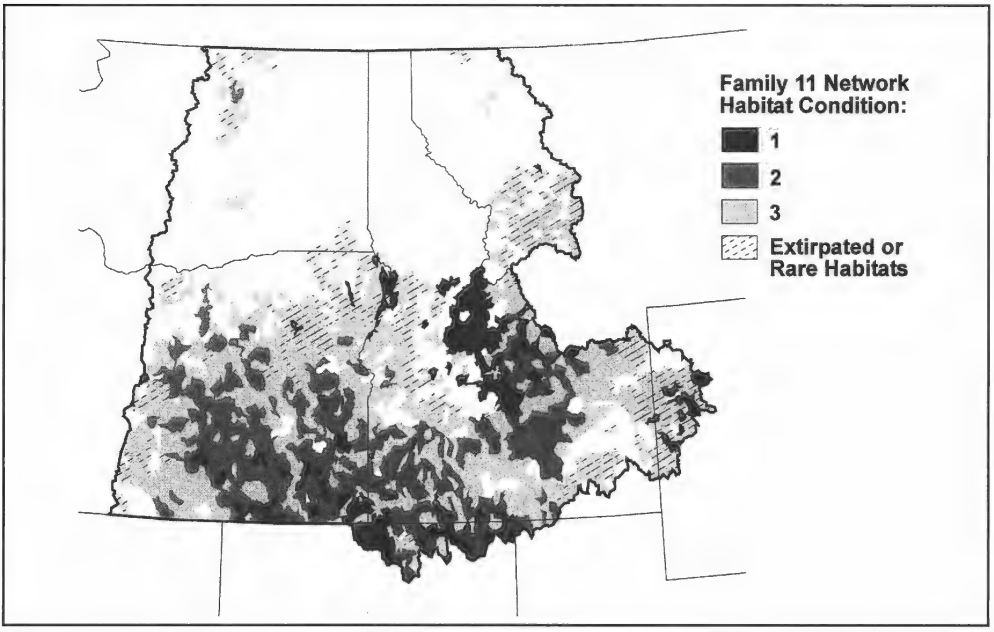

Figure 5. Network for Family 11, composed of sagebrush habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

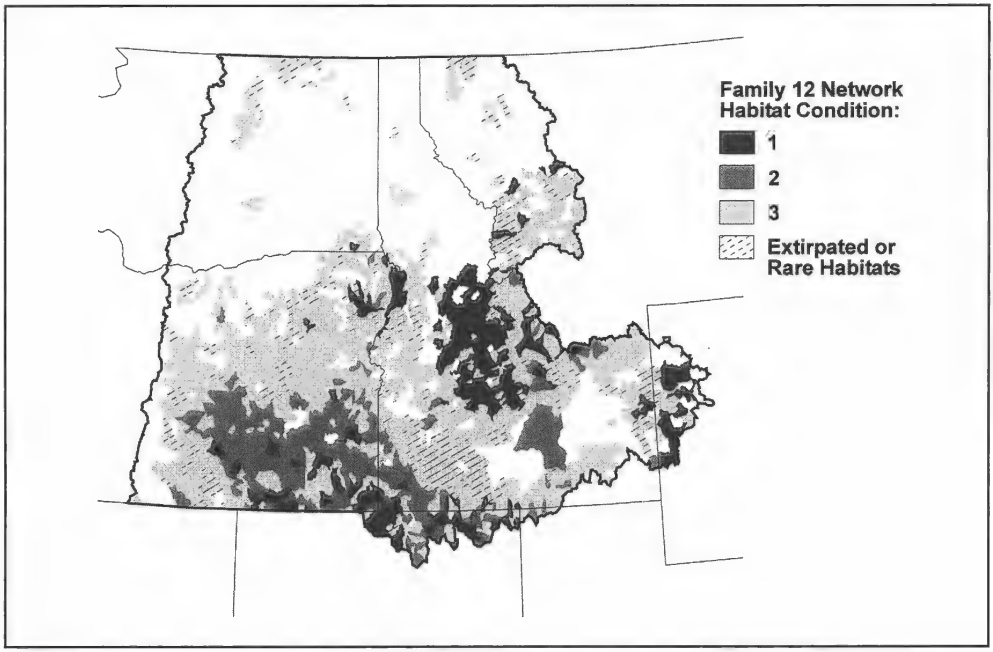

Figure 6. Network for Family 12, composed of open-canopy sagebrush and grassland habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

that wilderness areas, roadless areas, National Parks, and Condition 1 watersheds currently make a small contribution to available habitat for the five Families, and that most of this contribution is in lands that are not actively managed.

A second, complementary pattern is that most habitats for Families 1, 11, and 12 exist at lower elevations in sub-optimal condition (Condition 2 or 3). Moreover, watersheds in Conditions 2 and 3 have small overlap with wilderness areas, roadless areas, or National Parks, and typically have been subjected to intensive timber harvest, intensive grazing by livestock, extensive road development, and widespread fire suppression. This same pattern also exists for Families 2 and 4, but is not as strong as that for Families 1, 11, and 12. In combination, the above results suggest that any conservation approach based solely or mostly on maintenance of Condition 1 watersheds, without explicit consideration for managing watersheds in Condition 2 or 3, would not address the composite needs of species in the five Families.

A third important pattern is the relatively small percentage of watersheds in Condition 2, where reduced resiliency and quality may limit the long-term presence and suitability of habitat. Although watersheds in Condition 2 make up a relatively small percentage of all watersheds, this condition implies the need to restore disturbance regimes in a manner that can improve resiliency, combined with a need to reduce road density and human disturbance activities in a manner that can improve quality. Consequently, watersheds in Condition 2 may often require active restoration to improve habitat quality and resiliency while maintaining habitat abundance.

Finally, a fourth and perhaps most compelling pattern is the dominance of Condition 3 watersheds for all Families, and the large percentage of these watersheds where habitats have been extirpated. This pattern implies that (1) habitat conservation is critical to protection of small, remnant habitats that dominate many of these watersheds; and (2) habitat restoration is key to increasing the typically low habitat abundance within these watersheds, and to improving the weak habitat connectivity among these and other watersheds. In particular, the restoration of extirpated old-forest,

sagebrush, or grassland habitats will require long time periods, focused planning, sustained implementation, and explicit consideration of the composite needs of species in the five Families within and among the Condition 3 watersheds.

Relation of Theory to Network Characteristics

The connection between principles of conservation biology and their application is not always clear (Doak and Mills 1994). In particular, much debate has focused on landscape issues of patch size, quality, resiliency, connectedness, and human disturbance effects in relation to meeting species needs. For example, whether habitats should be composed of a large number of small reserves (Simberloff and Abele 1976a, 1976b) versus a small number of large reserves (Diamond 1976) is one simplistic illustration of this debate. Such debate continues today, and is magnified by the question of how well theory can be used to meet the composite needs of many species across large landscapes (Shafer 1990, Harrison and Fahrig 1995).

Despite this debate, the combination of theory and empirical data to date provides compelling evidence that a species' persistence depends on suitable habitats of sufficient size and connectedness, sustained indefinitely over large areas that encompass all or most of the species range (Shafer 1990). These conditions buffer the otherwise negative effects of environmental variability, demographic stochasticity, inbreeding depression, and other deleterious processes that cause extinction of small or isolated populations (Burgman et al. 1993).

In that context, our broad-scale network provides both a theoretical and a practical foundation for conservation planning for groups of species that are of conservation focus. Specifically, the network could be used to maintain habitats in a relatively unchanged state from historical conditions (Condition 1), to improve habitats where quality and resiliency have declined (Conditions 2 and 3), to restore habitats in areas of extirpation or low abundance (Condition 3), and to improve connectivity where spatial gaps have developed (Condition 3). Such characterization is a coarse-filter approach, developed for a large set of vertebrates of conservation focus, as summarized over a vast area of the Interior Northwest, for potential use in conservation planning.

For example, a management strategy could be developed from the network information to maintain historical fire regimes in Condition 1 watersheds, helping perpetuate this Condition. Another complementary strategy could emphasize the reduction of road-associated effects in Condition 2 and 3 watersheds, to improve habitat quality and resiliency. A third strategy could focus on conservation of rare habitats in Condition 3 watersheds, with emphasis on protection from imminent management threats, such as those posed by stand-replacing wildfires or by intensive timber harvest. A fourth strategy could outline long-term treatments needed to restore extirpated habitats, thereby improving connectivity over time.

Our network also provides a basis for testing theory as part of adaptive management experiments (Walters 1986). We are unaware of any research hypotheses that have been tested to evaluate the theory, empirical accuracy, and management implications associated with habitat conditions for such a large landscape and large number of vertebrates as that analyzed here. Unfortunately, past research on species of conservation focus, both within the Basin and elsewhere, has largely been fine-scale, single species, observational, not replicated, conducted over short time periods, and not designed to incorporate habitat conditions and associated management actions as treatments.

By contrast, our characterization of a broad-scale network of habitats provides an explicit opportunity for testing multi-species research hypotheses for vertebrates of conservation focus across an extremely large landscape. For example, researchers could hypothesize about multi-species, community-level relations for these terrestrial vertebrates in relation to our habitat conditions, and design and conduct validation research to test these hypotheses. Results of such validation research, if replicated across large areas of the Basin, could provide a rigorous test of the efficacy of our coarse-filter approach for management applications.

Without such multi-species conservation planning and research, the likelihood of extirpation for many vertebrate species in the Basin is high, both for the current time period and under projected management (Raphael et al. 2001). We urge managers and researchers to consider these implications in their future conservation and research designs.

Acknowledgements

Tom Mills, Tom Quigley, Becky Gravenmier, and Russ Graham provided essential leadership and administrative support for our analysis. The Pacific Northwest Research Station and other ICBEMP funding sources from the USDA Forest Service and USDI Bureau of Land Management supported this work. Karen Oakley and Sara Wesser provided helpful reviews. Data and maps on habitat conditions and the associated documentation and source materials are available from the senior author and the ICBEMP website: www.icbemp.gov. Source materials from earlier publications also are available on the ICBEMP website.

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Received 20 March 2001
Accepted for publication 14 September 2001

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George P. Keister, Jr.,[1] Oregon Department of Fish and Wildlife, 2995 Hughes Lane, Baker City, Oregon 97814

and

Walter A. Van Dyke, Oregon Department of Fish and Wildlife, 3814 Clark Blvd., Ontario, Oregon 97914

A Predictive Population Model for Cougars in Oregon

Abstract

Cougar numbers in Oregon declined between 1928 and 1961, primarily due to excessive harvest from the bounty system. Cougars were classified as a game mammal in 1967 and sport harvest began on a limited basis in 1970. Because determining population size of cougars by direct count methods is impractical, indirect methods to evaluate status are needed. We analyzed harvest levels, damage complaints, and data obtained from harvested cougars to evaluate their status in Oregon. Biological data obtained from Oregon and other states were used to develop a density dependent model of the cougar population of Oregon. As indicated by the model, numbers increased from an estimated low of 214 in 1961 to 2,830 in 1992, which coincided with other indicators including increased livestock damage, human safety complaints, and sport harvest. The model indicated higher mortality rates for hunted populations and lower proportions of juvenile cougars in populations at carrying capacity. For the modeled population in 1993, sport harvest rates of 5.4% allowed a 5% annual growth. A sport harvest of 10% of the population and a total mortality rate of 35% was needed to stabilize that population. The model predicted that if sport harvest ceased, cougar numbers would increase until carrying capacity is reached in the year 2009. We believe the model is a useful tool to summarize existing data, explore effects of hypothesized management plans, and adaptively aid in management decisions. The model can be adapted to other states if appropriate population parameters can be determined.

Introduction

Historically, cougars (*Puma concolor*) were considered an undesirable predator in the western United States. Perceived as a threat to livestock, state and federal agencies implemented programs that resulted in a substantial reduction in cougar numbers and elimination of cougars from much of their historic range (Dixon 1978). In Oregon, a bounty system for cougars existed until 1961. Statistical analyses in the early 1970s, based on population estimates from harvested cougars, indicated that the statewide population in 1961 was extremely low and without protection, cougars would likely have been extirpated from Oregon by the early 1970s (Warren W. Aney, 1973, unpublished letter on file at Oregon Department of Fish and Wildlife, Portland).

Cougars were afforded game mammal status by the 1967 Oregon Legislature and no season was authorized until 1970. Limited hunting began in 1970 when 25 tags were authorized, primarily in response to livestock damage concerns in a small area of northeastern Oregon. Since then, livestock damage complaints, cougar sighting reports, and past harvest history have been the primary factors used to recommend hunting seasons. Legal challenges to cougar hunting in 1988 prompted the Oregon Department of Fish and Wildlife (ODFW) to look for additional ways to assess the status of cougar populations.

Because of their low densities, secretive nature, and large home ranges, wildlife managers and researchers have struggled with the problem of accurately measuring cougar populations. We are unable to measure, on an annual basis, most of the parameters necessary to know precisely what is happening with local cougar populations at all times. Our poor monitoring capability is because methods are simply not available to measure cougar populations with the precision possible for other species (e.g. Douglas-fir trees, bald eagles, mule deer, pronghorn) and money is rarely available to use the methods that are available. The best population estimates come from intensive field work (Lindzey 1987). Track counts have been used in several areas (Ashman et al. 1983, Neal et al. 1987). However this method only provides an index to population, depends on a good tracking substrate such as snow or dust, and has been costly. Most commonly, radio telemetry has been employed in mark-recapture and complete capture studies. Several years are necessary to determine

[1]Author to whom correspondence should be addressed. E-mail: glwkeist@oregonVOS.net

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a population estimate. Both methods are costly and time consuming because of the logistics involved in capturing a high proportion of the population in a large area of rugged habitat. In addition, results of such studies may represent only a small portion of the state. We employed statistical analysis and population modeling to assess status of cougar populations throughout the state. We relied on data accumulated over many years and results of studies in Oregon and other states. Whereas it appears there are numerous pieces of unrelated information relative to cougars, through population modeling we can combine this information in a way that approaches reality and better explains cougar population performance. Our objectives for this paper were to: 1) analyze historical data to help determine status of cougar populations in Oregon and 2) develop a biologically intuitive model that relies on data that are readily available and which can be created and used by managers.

Study Area

Habitats in Oregon are diverse. Temperate coniferous forests dominate the Coast Range and western slope of the Cascades. Several interior valleys of western Oregon are used for agriculture, such as grass seed production, fruit and vegetable farming, dairy farming, and livestock operations. Most (87%) of the human population (~3,000,000) reside in the western interior valleys (Levine 1995). East of the Cascade Mountains, habitats are drier and include coniferous forests on the east slope of the Cascade Range and in the Blue Mountains; shrub steppe dominates the southeastern third of the state. Intensive agriculture occurs at lower elevations in the Columbia and Snake River basins.

Cougars are distributed statewide except for areas where agricultural practices and human development have altered habitat suitability for cougars and their prey. For the most part, cougars are closely associated with deer and elk distributions in the state. In the 1990s, reports to ODFW of cougars in urban and suburban areas became increasingly common.

Methods

A mandatory check-in of all cougars taken during hunting seasons in Oregon was instituted in 1970, while check-in of cougars killed on depredation has occurred since 1980. Reproductive status, stomach contents, age, and sex of harvested cougars were determined at the ODFW Wildlife Laboratory in Corvallis.

Analysis of Harvest and Complaint Data

We used regression analysis to examine hunter harvest and success and to determine if there were significant trends through time. Several dependent variables (bountied cougars, sport-harvested cougars, hunter success) were individually regressed against time. The analysis was broken into two periods: 1) 1928-61 during the cougar bounty years, and 2) 1970-92 when cougars were hunted as a big game mammal with an annual limit on the number of tags issued per hunt unit. In addition, "other losses" (e.g. depredation, accidents), 1980–1992, and damage complaints, 1970–1992, were used as dependent variables in simple regressions against time. Relationships between dependent and independent variables were considered significant at $P \leq 0.05$. Damage complaints most commonly included complaints to ODFW from depredation on livestock and sightings of cougars on private property where there were concerns for human safety.

Biological Parameters

Many biological parameters affecting cougar populations must be considered in model development. Factors that affect productivity were age at first breeding, birth interval, litter size, sex ratio, and longevity. Factors affecting age-specific mortality included natural and human-caused mortality (e.g. sport or depredation harvest, auto collision). Several studies of cougars in the western states and Canada have reported results relative to these factors (Table 1). We used plausible values for these parameters based on data collected mostly in Oregon or representative of cougar populations throughout their range.

Seidensticker et al. (1973) believed young females usually breed only after establishing a home range. Data collected in Oregon support that hypothesis (Trainer and Golly, 1989). Based on these data and results found elsewhere (Table 1), we assumed that all females > 3 yr old and 69% of those between 2 and 3 yr of age breed. Thereafter, females normally breed soon after loss of kittens or dispersal of their litter (Lindsey 1987) causing the birth interval to vary (Table 1). We assumed

TABLE 1. Factors affecting cougar populations and the range of values reported by various authors.

Productivity factor	Values reported	Source
Age at first breeding	16 - 29 mo	Eaton and Velander 1977
	27 - 33 mo	Young and Goldman 1946
	29 mo	Rabb 1959
	22 - 24 mo	Ashman et al. 1983, Logan et al 1986
	20 mo	Lindzey 1987
Birth interval	24 mo	Johnson and Couch 1954
	24 mo	Robinette et al. 1961
	12-20 mo	Hornocker 1970
	17.4 mo	Ashman et al. 1983
	18 - 24 mo	Lindzey 1987
	12 - 17 mo	Lindzey et al. 1994
	19.9 mo	Anderson et al. 1992
Litter size	2.0	Johnson and Couch 1954
	2.5	Hornocker 1971
	2.5	Eaton and Velander 1977
	2.6	Anderson 1983
	2.8	Ashman et al. 1983
	2.7	Logan et al. 1986
	2.4	Hemker et al. 1982
	2.4	Lindzey et al. 1994
	2.8	Toweill et al. 1984
	2.4	Toweill et al. 1988
	2.4	Trainer et al. 1993
Sex ratio (male:female)	100:100 (population)	Johnson and Couch 1954
	100:100 (population)	Tanner 1975
	125:100 (kittens)	Ashman et al. 1983
	125:100 (harvest)	Anderson 1983
	100:100 (capture)	Logan et al. 1986
	120:100 (harvest)	Toweill et al. 1984
	150:100 (harvest)	Trainer et al. 1993
Longevity	18 yr	Anderson 1983
	15-18 yr	Young and Goldman 1946
	10 yr	Johnson and Couch 1954
	7 yr	Logan et al. 1986
	12-17 yr	Trainer et al. 1993
Age Specific Mortality Rates	Adults—10%	Johnson and Couch 1954
	Kittens—26%	Tanner 1975
	Adults—12%	Tanner 1975
	Overall—32%	Robinette et al. 1977
	Kittens—28%	Ashman et al. 1983
	Overall—30%	Ashman et al. 1983
	Overall—26-28%	Lindzey et al. 1988
	Overall—12%	Anderson et al. 1992

an average birth interval of 19 mo, which is equivalent to a 63% (12 mo/19 mo) annual pregnancy rate.

Documented litter sizes are somewhat consistent among existing studies (Table 1). Litter size can be indicated by counting corpora lutea in

harvested females each year. However, we do not know how long corpora lutea may last for cougars and corpora lutea counts tend to over-estimate litter size. We, therefore, used a value of 2.4 kittens/litter in our model because it was based on fetuses present in pregnant cougars rather than corpora lutea (Trainer et al. 1993). It was the most recent and complete measurement of litter size for cougars in Oregon and was similar to values reported elsewhere.

Sex ratios at birth are commonly equal whereas sex ratios in the harvest are often skewed toward males (Table 1) due to either higher vulnerability of males or selection for males by hunters. In the interest of simplicity, we assumed equal sex ratios.

A wide range of longevity values has been reported (Table 1). In Oregon, 22 of 1,089 (2%) cougars aged from 1987 through 1992 were between 12 and 17 yr of age (Trainer et al. 1993), therefore we used a maximum age of 17 yr for this model.

Age-specific, natural mortality rates are difficult to assess accurately. Specific mortality rates are not available for each age (Table 1), but are necessary for modeling. Several authors agree that kittens, dispersing subadults, and very old cougars experience higher mortality than prime-aged adults (Tanner 1975, Russell 1978, Anderson 1983). For our model, the following natural mortality rates were assumed: 5% for kittens (<1 yr - old); 20% for 1, 2, and 10-13 yr-old; 8% for prime-aged adults (3-9 yr-old); 25% for 14-17 yr-old; and 100% for 18 yr-old.

Human-caused mortality includes losses due to accidents (e.g. road kills), cougars killed on livestock depredation and safety complaints, illegal harvest, and sport harvest. These losses must be accounted for and distributed among age classes at different rates from natural mortality. Records of "other losses" (e.g. accidents and depredation kills) in Oregon have been kept since 1980 and ranged from 10 in 1983 to 50 in 1993. To account for such sources of mortality before 1980 and after 1993, "other losses" were estimated at an annual mortality rate of 2.3% of the adult population, which provided close calibration between predicted and observed mortality for the 1980 through 1993 period.

Losses of cougars from illegal harvest have been reported (Anderson 1983); however, actual rates of illegal kill have been difficult to document. Anderson et al. (1992) reported that two of 49 radio-marked cougars in an unhunted population in Colorado were illegally killed from 1981 through 1988. Neal et al. (1987) reported 11% to 16% of 19 marked cougars were lost illegally in Northern California over a two-year period. In Washington, eight of 26 marked cougars were illegally killed from 1974 through 1986 (Dave Brittell, 1987, Washington Department of Fish and Wildlife, personal communication). Average annual illegal mortality in an ongoing study in southwestern Oregon was 6.2% for 65 radio-collared cougars from 1993 through 1998 (DeWaine H. Jackson, 1999, Oregon Department of Fish and Wildlife, personal communication). In northeastern Oregon, one of 27 collared cougars was illegally killed between 1989 and 1994 (Mark G. Henjum, 1995, Oregon Department of Fish and Wildlife, personal communication). For our model, a value of 3.5% of the adult population was chosen to represent illegal kill for the entire state.

Legally harvested cougars were added to "other losses" and estimated illegal kill to obtain total human-related loss. Based on ages of 1,089 cougars killed in Oregon between 1987 and 1993 (Trainer et al. 1993), human-related loss was apportioned to the 0 to 1 yr age class at 5.6%; and to the 1 to 2 yr age class at 11.4%. However, for adults (age 3 to 17 yr), we assumed losses in each age class occurred in proportion to availability of that age class in the population.

Model Development

A mathematical model of Oregon's cougar population was developed in the form of a life table using spreadsheet software on a microcomputer. To create a model that behaved realistically during and after bounty years, we began the model in 1928 when numbers of bountied cougars were relatively high. Number of cougars in each age class was initially estimated based on ages of cougars checked in during 1987–1993 (Trainer et al. 1993). We used iteration, that is we ran the model several times changing the beginning age ratios each time based on results, to determine the age distribution that best represented the 1928 population and its harvest pressure. Input for each year included legal (i.e. sport or bounty) harvest, other losses, and illegal kill. Number of cougars in each age class, except kittens, was determined

by starting with the number of cougars in the prior age class, during the previous year and adjusting for age specific mortalities (both natural and human-caused). To calculate number of kittens (young born and surviving for one year) in a particular year, number of breeding adults surviving from the previous year was multiplied by proportion female, proportion pregnant, and litter size. Number of kittens was then adjusted for mortality. We assumed that kittens died if their mother died during the first year of the kitten's life.

An independent estimate of population was used to calibrate the population model. Warren W. Aney (1973, unpublished letter on file at Oregon Department of Fish and Wildlife, Portland) used formulas provided by Johnson and Couch (1954) to calculate the Oregon population based on harvest (1913 - 1961). A statewide population estimate for 1961 was 214 cougars. Total population for the starting year of 1928 was adjusted in the model until the 1961 population was as near as possible to 214 without causing the population to crash thereafter. The 1961 population estimate was the only and best available and indicates the population in the state was very low, but not extinct.

We assumed that cougar populations could not grow indefinitely. Tanner (1975) estimated intrinsic growth rates for several prey species and their predators using differential equations. He determined that for the cougar-deer predator/prey system, equilibrium can be achieved when cougars are limited by deer numbers if deer numbers are low, or by a certain maximum predator population if deer numbers are high. Seidensticker et al. (1973) believed that cougar density in the Idaho Primitive Area was probably controlled by social behavior interacting with habitat factors (e.g. vegetation and topography) and prey numbers to produce maximum densities characteristic of particular areas and habitat types. Cougars are territorial and males defend that territory against other males, often killing them as well as kittens (Dixon 1978). Adult females are occasionally killed by other cougars (Lindzey 1987). As density increases, territories overlap more, probably causing a higher incidence of intraspecific predation.

Cougar densities have been documented at 1.0 to 1.6/100 km^2 in Nevada (Ashman et al. 1983) and as high as 5.2/100 km^2 in eastern Fresno County, California (Neal et al. 1987), 6.7/100 km^2 in Black Gap, Texas (Parsons 1976), and 9.2/100 km^2 in Glenn and Colusa Counties, California (Sitton 1972). In Oregon, preliminary study results indicate present densities of 3.9/100 km^2 in the northeastern Blue Mountains (Mark G. Henjum, 1995, Oregon Department of Fish and Wildlife, personal communication) and 5.4/100 km^2 in the southwestern Cascades (Jackson et al. 1999). To allow the model to behave in a density dependent manner, a maximum population was estimated for Oregon by assigning maximum densities to each region of the state based on findings of studies in Oregon and other areas of similar habitat in the West. Maximum density estimates for western Oregon ranged from 8.0/100 km^2 in southwestern Oregon to 4.0/100 km^2 in northwestern Oregon. In eastern Oregon, maximum density estimates ranged from 1.6/100 km^2 in southeastern Oregon to 3.2/100 km^2 in central Oregon, and 3.9/100 km^2 in the Blue Mountains of northeastern Oregon. A weighted average (based on area of each region in Oregon) of 3.2 cougars/ 100 km^2 was obtained for the state, which corresponds to a maximum possible population of 8,064 cougars.

To incorporate density dependence into the model, a density factor (DF) was assumed when the population reached 75% of the 8,064 cougar maximum. The DF was used to increase age specific, natural mortality rates (mortality rate x DF) and decrease productivity (proportion pregnant each year/DF). The DF depended on the proportion of maximum population (M) and was calculated using a quadratic equation ($DF = 2.8–4.9 M + 3.5 M^2$). The quadratic equation was determined algebraically to fit a curve that produced a DF that increased as the population approached maximum so that when applied to productivity and mortality, a logistic curve characteristic of a population growing to carrying capacity was created. We applied the density factor at 75% of the maximum population because we felt 75% would be a high enough density in the wild to begin to influence lower productivity and higher mortality. However, we built into the model the ability to readily change parameter values so we can modify the model as we learn more information or want to try different assumptions. Thus, other equations for DF or how and when DF is applied can be explored. In fact, for purposes of comparison, we calculated a different quadratic equation that was applied at 50% of maximum population. The difference between the two curves was trivial.

We conducted sensitivity analysis to determine which factors were most important in affecting population performance. We varied proportion pregnant, litter size, natural mortality rates, and rates of "other losses" and illegal kill by 10%, then noted the resulting change in cougar population after 1 yr and 20 yr.

Results

Data Analysis

Number of cougars taken annually under the bounty system peaked at 337 in 1930 and thereafter declined to a low of 26 in 1961. Analysis of harvest data between 1928 and 1961 showed a significant decline in cougars bountied (Figure 1). Since limited sport harvest began in 1970 (Figure 2), annual harvest increased significantly through 1992 from 10 in 1970 to a high of 187 in 1992. Hunting success averaged 41% during the period and did not decline signigicantly. Since 1970, damage complaints increased significantly (Figure 3), as did "other losses" (Figure 4).

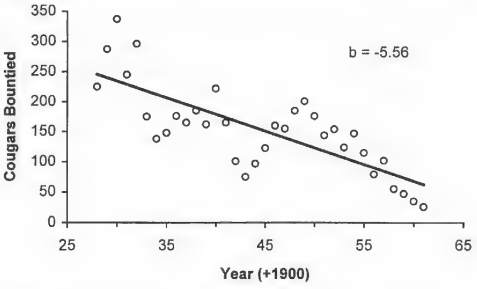

Figure 1. Simple linear regression of number of cougars bountied vs. time in Oregon ($r^2 = 0.59$), 1928-1961.

Population model

The modeling process allowed the logical combination of seemingly unrelated information into an understandable form that helped explain cougar population trends and status in Oregon. The model indicated over-exploitation of the population during the period of the bounty system, with the population reaching a low in 1961 and rebounding under limited harvest regulations to a high of 2,830 in 1992 (Figure 5).

The model was used to predict population performance under four scenarios (Table 2). For 1993 conditions in Oregon, hunted and below carrying capacity, 5.4% of the modeled population was legally harvested. The total mortality rate, kitten mortality rate, and mortality rates for dispersing juveniles (1-2 yr-old and 2-3 yr-old) were greater than for an unhunted population below carrying capacity (Table 2). For an unhunted population below carrying capacity, mortality rates were reduced to natural mortality rates for 1-2 yr-old,

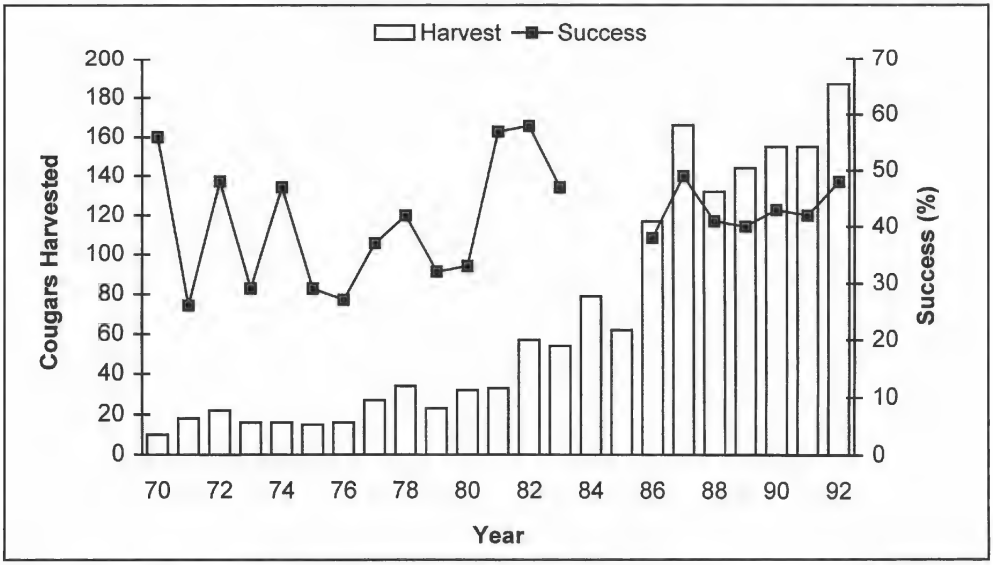

Figure 2. Number of harvested cougars and hunter success (%) in Oregon, 1970-1992 (No hunter survey in 1984 and 1985).

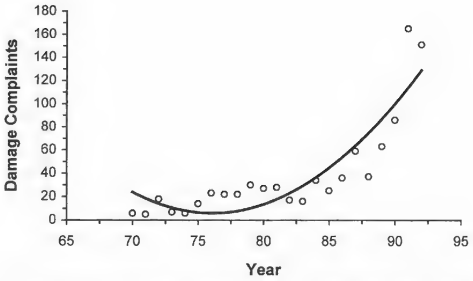

Figure 3. Polynomial regression of cougar damage complaints in Oregon vs. time ($r^2 = 0.79$), 1970-1992.

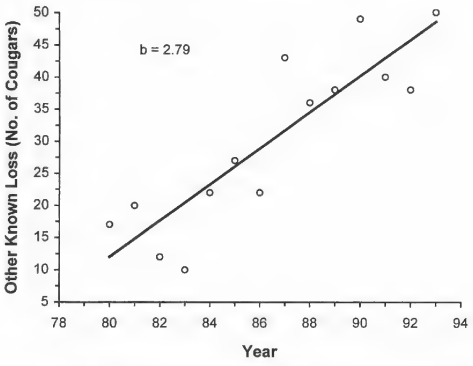

Figure 4. Simple linear regression of known cougar mortalities from other than legal harvest in Oregon ($r^2 = 0.73$), 1980-1992.

and adults between 3 and 9 yr (Table 2). However, the mortality rate for kittens was higher (19%), because in addition to the 5% direct natural mortality built into the model, kittens also died when adult females died of natural causes. The modeled population stabilized at carrying capacity through a combination of decreased productivity and increased mortality (Table 2).

TABLE 2. Characteristics of a hypothetical cougar population in Oregon determined by a simulation model.

	Population Status			
	Below carrying capacity		At carrying capacity	
	Hunted	Unhunted	Hunted	Unhunted
Mortality Rates (%)				
Total	30	24	29	26
Kittens	31	19	27	20
1 yr	23	20	29	32
2 yr	27	20	31	32
3-9 yr	16	8	16	13
10-13 yr	27	20	31	32
14-17 yr	35	25	36	40
Birth Interval (mo)	19	19	26	30
Age Structure (% of population)				
Kittens	26	27	23	23
1-2 yr	19	18	17	15
3-17 yr	55	55	60	62

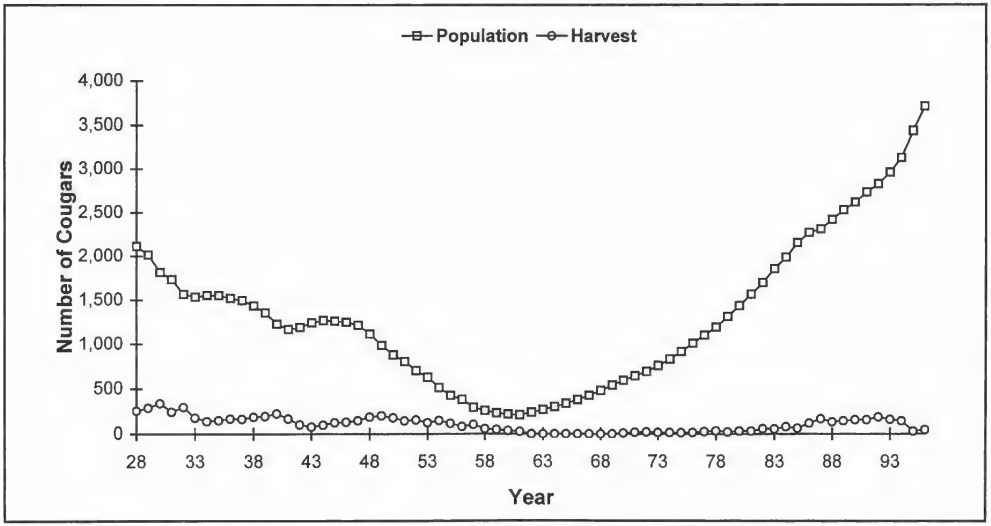

Figure 5. Cougar population, as determined from simulation modeling, and harvest in Oregon, 1928-1992. Cougars were bountied until 1961. The season was closed until 1970 when limited hunting began.

Age distribution of the modeled population depended primarily on the status relative to carrying capacity rather than on whether it was hunted (Table 2). Proportion of 0-2 yr-old animals was greatest for populations below predicted carrying capacity (45% juveniles: 55% adults). At carrying capacity, age structure of a hunted population (40% juveniles: 60% adults) was similar to an unhunted population (38% juveniles: 62% adults).

Sensitivity analysis showed that 10% changes in litter size and proportion pregnant could change the predicted population after 20 yr by 159% and 143%. A 10% change in natural mortality rate had a 117% effect on population performance. In contrast, 10% changes in "other losses" and illegal kill had only 16% and 22% effects on population.

Discussion

Our analysis of harvest data agreed with Warren W. Aney (1973, unpublished letter on file at Oregon Department of Fish and Wildlife, Portland), who used linear regression of number of cougars bountied versus time (1913–1961) to conclude that if the state's cougar population had continued to decline at the same rate, it would have reached zero by 1973. Cessation of the bounty system in 1961 and limited hunting, which began in 1970, resulted in significant increases in sport harvest, with stable hunter success, and increases in damage complaints and "other losses". Significant increases in harvest, "other losses", and damage complaints indicate cougar populations in Oregon have grown and adds support to the validity of the model.

Increases in damage complaints and "other losses" may be somewhat influenced by increases in the state's human population. The state's population increased from ~2,092,000 to 3,082,000 (47%) from 1970 to 1994 (Levine 1995). But in the 11 eastern counties that constitute about half the land area, the human population increased only 26% (~176,000), 1970–1994. In addition, land ownership patterns are such that most human habitation is in more developed, lowland areas and not in historic cougar habitat. In Oregon, 55% of the land is publicly owned (Levine 1995), most of which is located at higher elevations; private lands are primarily located at lower elevations. While human populations have increased, particularly on the west side of the Cascades and in central Oregon, that increase has mostly been confined to those lower elevation areas.

For model development, we input basic biological data relative to productivity and age specific mortality obtained from numerous sources, mostly Oregon. We then compared population performance (total population mortality and population age ratios), as calculated by the model, to results from several different sources.

Comparison of studies of wild cougar populations with model simulations is complicated for several reasons. Researchers are often unable to monitor all members of a particular population and small sample sizes are common. Kitten mortality is often underestimated because kittens are usually not found until several months after birth. Population status (below or at carrying capacity) is often not known or stated in study results. In addition, researchers have sometimes not defined ages for kittens, juveniles, and subadults and have sometimes used these terms to represent different aged animals in different studies.

In spite of difficulties in precisely measuring wild cougar populations and comparing with model simulations, results of several studies allow some comparisons of population performance in terms of mortality rates and age composition. We calculated mortality rates from data presented by Hornocker (1970) for a cougar population in a central Idaho wilderness during 1964–69. That population received light hunting pressure during the study, but was hunted for bounty prior to the late 1950s. Therefore, this Idaho population likely represented an unhunted population below carrying capacity. Overall mortality was 17%, with 21% for juveniles and 14% for adults. From data collected in the same area by Seidensticker et al. (1973), we calculated a mean of 27% juveniles in the population between 1964 and 1972. These results are similar to mortality rates and age composition determined by our model for a hypothetical unhunted population below carrying capacity in Oregon. Overall mortality was 24% with 19% for kittens, 20% for 1-2 yr-old, and 8% for adults (3-9 yr-old). The population comprised 27% kittens and 18% 1–2 yr-old (Table 2). However, Anderson et al. (1992) calculated a lower overall mortality rate (12%) for a population in Colorado which was unhunted during the study, but had been hunted before the study. For cougars captured during that study, 46% were kittens and 21% were 1–2 yr.

Our model generally agreed with findings from several hunted populations and mortality rates were greater than for unhunted populations. For a hunted population below carrying capacity, the model predicted mortality rates of 30% total and 31% for kittens, and an age ratio of 26% kittens and 19%, 1-2 yr-old (Table 2). These proportions suggest an age ratio of approximately 38% (26.0% + 9.5%) for juveniles <1.5 yr-old and 45% (26% + 19%) for juveniles < 2 yr-old. In a hunted population in Nevada, Ashman et al. (1983) likewise observed 30% overall mortality with 28% mortality of kittens, and estimated that 40% of the population were kittens still with their mothers (probably 1 mo to 16-24 mo of age). Overall mortality rates in Utah were similar at 32% for a hunted population (Robinette et al. 1977) and 26-28% for a population with limited hunting (Lindzey et al. 1988). For the same population, we calculated from data presented by Lindzey et al. (1994) a mean of 41% juveniles (0–1.5 yr) for 1979 through 1987. Logan et al. (1986) estimated that a hunted population in Wyoming consisted of 50% juveniles (0-24 months).

It is important to note that the model we developed was deterministic rather than stochastic. There are parameters that vary from year to year with weather, such as survival, productivity, susceptibility to human harvest (varies with snow conditions), or disease. Whereas we can measure harvest from year to year, we have no way to measure the other variables on an annual basis. The rest of the variables were determined over several years from measurement of dead cougars or from intensive study in several locations or were assumed.

Management Implications

This model can be used as an adaptive tool to help make management decisions concerning cougars in Oregon. We used the model to answer several questions. One such question was: What would happen to the population if harvest continued at a particular level? To answer that question, we input the 1993 harvest of 160 cougars for each year after 1993. The model predicted that the cougar numbers would continue to grow initially at 5% annually then stabilize at a maximum by the year 2016 (Figure 6).

Because use of hounds for sport hunting of cougar was banned in Oregon in 1994, we asked

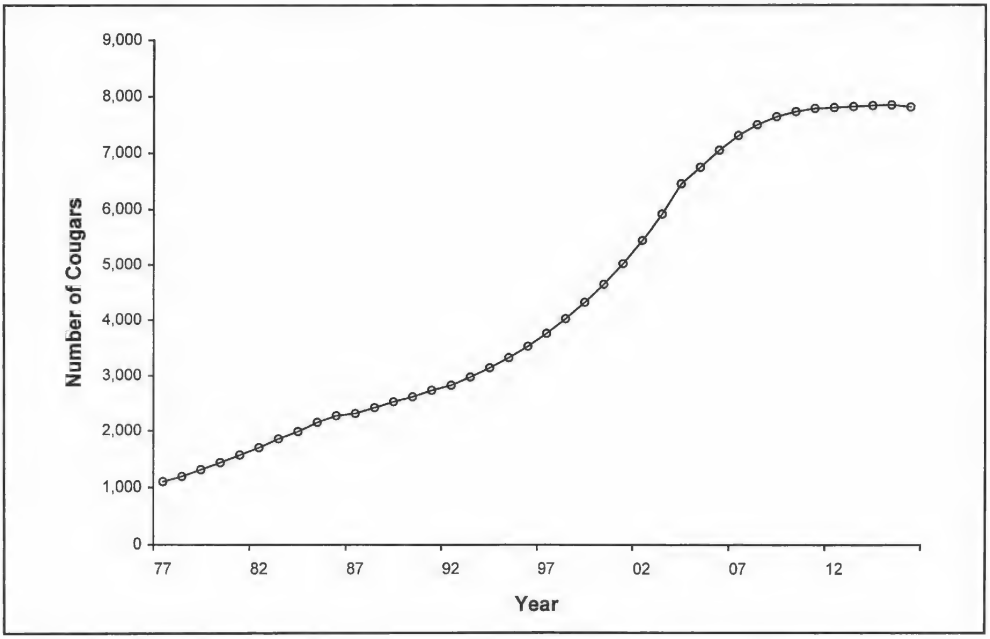

Figure 6. Modeled cougar population of Oregon with sport harvest held at 160 cougars/yr after 1992.

what would happen if sport harvest were discontinued after 1993 but other human-caused losses continued? The model predicted the population would initially increase at a 13% annual rate. The rate of increase would decline by year 2000, when density dependency became a factor, and the population would stabilize in the year 2009 at about three times the 1993 level. If this hypothesized population increase is correct, we should see further increases in human-cougar interactions that could include increased damage complaints, more cougars killed as a result of depredation, more sightings, more instances of cougars in urban and suburban areas, and possibly attacks on humans.

Another pertinent question was: What harvest was necessary to stabilize the population at the 1993 level? To answer that question, harvest rates were adjusted after 1993 until the modeled population stabilized near the 1993 estimate of 2,960. We found that an annual sport harvest rate of 281 cougars (10% of the population) and a total mortality rate of 35% would be necessary to stabilize the population. Population performance could be tested in the future if methods allowed a significant increase in sport harvest in Oregon. Harvest rates could be increased to the level necessary to stabilize or reduce the population as indicated by the model. We would expect a leveling or decrease in damage complaints, depredation kills, sightings, and other human-cougar interactions.

As knowledge increases about those parameters that control the model or as conditions change, the model will need adjustment. Intensive field research across the state could provide independent population estimates that could be used to re-calibrating the statewide model and would allow development of more localized models for smaller areas of the state. Sensitivity analysis indicated that of those factors examined, productivity (i.e. proportion pregnant and litter size) and mortality rates had the greatest effect on population performance over time; therefore, emphasis should be focused on determining those rates. Productivity, mortality rates, and age ratios measured in the field could be compared to population performance predicted by the model. As habitat conditions and prey populations change, carrying capacities for cougars may change, affecting the maximum density function in the model.

We believe this model has application for other states that manage cougars. Reproductive rates, age-specific mortality rates, rates of illegal kill and depredation loss, estimates of maximum density, and some knowledge of the population level and trend are needed to model those cougar populations.

Acknowledgements

We thank R. E. Anglin, M. Conner, S. R. Denney, N. Hartmann, M. G. Henjum, D. H. Jackson, T. W. Keegan, F. Lindzey, E. C. Meslow, H. Quigley, S. J. Riley, C. E. Trainer, C. A. Wheaton, and G. Witmer for reviewing previous drafts of this manuscript.

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Received 13 March 2001
Accepted for publication 3 August 2001

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Dana E. Bailey, Daniel K. Rosenberg,[1] Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries & Wildlife, Oregon State University, Corvallis, Oregon 97331,

William Fender, Dorothy McKey-Fender, Soil Associates, 835 Ashwood Ave., McMinnville, Oregon 97128

and

Judy Jacobs, U.S. Fish and Wildlife Service, 2600 SE 98th Avenue, Suite 100, Portland, Oregon 97266

Patterns of Abundance and Habitat Associations of Earthworms in Remnant Forests of the Willamette Valley, Oregon

Abstract

Among the most pervasive introduced animal taxa in North America are earthworms in the family Lumbricidae. Understanding their patterns of abundance is important in evaluating their potential impact on the native earthworm fauna. We examined the relationship of the abundance of introduced and native earthworm species, and compared soil and vegetative attributes associated with their abundance in five remnant forests within the Willamette Valley, Oregon. We detected two genera of native earthworms, *Toutellus* (78.5% of native earthworms) and *Argilophilus* (21.5%), collectively, in 7% of the excavated soil samples. We detected non-native lumbricids at all five remnants, in 86% of the samples, and we estimated an average of 1,136 kg of lumbricids/ha in the top 25cm of soil. We found a positive association between counts of lumbricids and the percent of organic matter and moisture content. Greater depth of surface organic matter and sloped terrain were associated with the presence of *Toutellus*. We found a positive association between abundance (counts/sample) of lumbricids and *Toutellus*. We found no direct evidence that the introduced earthworm fauna was impacting native earthworm species, although we failed to detect numerous native species that are presumed to be present in the Willamette Valley. We recommend an experimental approach, coupled with field observations that allow the estimation of species-specific detection probabilities, for future research into the potential impacts of introduced earthworms on the native fauna. This topic deserves further attention given the ubiquity of introduced earthworms in North America.

Introduction

Although unknown to most ecologists, there is a diverse earthworm fauna in North America (Fender 1995). Earthworms in North America are divided into two families, Lumbricidae and Megascolecidae. The Lumbricidae includes most of the introduced earthworm species in the western United States and are native to Europe. The Megascolecidae are distributed in the southern hemisphere and in northwestern North America, and include most native western North American species. The native earthworm fauna of the western United States contains at least 9 genera and 28 species, with many still undescribed (Fender and McKey-Fender 1990, Fender 1995). Over 20 introduced species have been described in this region (Fender 1985).

Three factors likely have influenced the biogeography of western earthworms. The Pleistocene glaciation eradicated many native earthworms over much of the continent although several species survived in glacial refugia (Fender 1995). Physical barriers to dispersal, including the arid region east of the Cascade Range and the Sierra Nevada, may also have been important. Finally, human migration introduced various European species onto the continent through ship ballasts, potted plants, and the fishing industry (Gates 1966, Fender 1995, Dymond et al. 1997).

Observations of native earthworms in a wide range of conditions led Fender (1995) to suggest that native species may have a much higher tolerance than introduced species for soils with high clay content and low pH, an avoidance for sandy soils, and a preference for compacted soils along game trails. Contrary to this view, Piearce (1984) found a negative relationship between compaction and occurrence of native earthworms, and suggested that reduced soil porosity would impede movement. Spiers et al. (1986) found higher abundance of the native earthworm genus *Arctiostrotus* in soils with pH of 2.6 to 6.2. This limited understanding of earthworm ecology, obtained from only a few studies, forms our current understanding of the relationships between native and introduced earthworms in North America.

[1]Author to whom correspondence should be addressed. E-mail: dan.rosenberg@orst.edu

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We used this existing research to formulate our hypotheses on the patterns of abundance and habitat associations of introduced and native earthworms in the Willamette Valley of western Oregon. Western Oregon is well suited for investigations on the potential impact of introduced earthworms on the native earthworm fauna because of the abundance and diversity of earthworms in the region. We predicted (1) a negative relation between abundance of introduced and native earthworm species; (2) that native species would be more selective of soil and vegetative characteristics than would introduced species; and (3) that native species would increase in abundance in response to the density of conifer trees, soil compaction, and percent clay in the soils.

Study Sites

We conducted our study in the Willamette Valley of western Oregon, located between the Cascade Range and the Coast Ranges. The climate of the Valley is typically mild with wet winters and warm, dry summers (Franklin and Dyrness 1973). We selected five remnant forests from twelve sites in which the Oregon giant earthworm (*Driloleirus macelfreshi*) was previously found. Three sites were excluded due to development and four sites were excluded because of restricted access. All five sampled sites were adjacent to farmed land, rivers, creeks, ponds, or sloughs, were ~70 m elevation, and ranged from 3 - 12 ha (Table 1). The dominant overstory consisted of Douglas-fir (*Pseudotsuga menziesii*), bigleaf maple (*Acer macrophyllum*), Oregon white oak (*Quercus garryana*), red alder (*Alnus rubra*), and Oregon ash (*Fraxinus latifolia*). Understory species included English ivy (*Hedera helix*), Himalayan blackberry (*Rubus discolor*), dull Oregongrape (*Berberis nervosa*), Pacific blackberry (*Rubus ursinus*), snowberry (*Symphoricarpos albus*), and western swordfern (*Polystichum munitum*).

Methods

Sampling

Within each of the five sites (remnant forests) we established an array of points from which we sampled earthworms and habitat characteristics. We sampled each of the five sites twice, from February-April 2000, when soils were moist and above freezing. For each of the two sets of samples, we randomly selected a distance and direction for the initial sample point. Each subsequent sample point (n=45 - 61 per site) was selected systematically, and spaced at 10-30 m depending on the size of the site. At each sample point, we excavated an area of 22 x 22 x 25 cm (~12,000 cm^3 soil removed) below the soil surface, following methods described by Zicsi (1962) and Dickey and Kladivko (1989). We counted the number of individuals of each earthworm taxon detected by hand-sorting the excavated soil (Dickey and Kladivko 1989, Callaham and Hendrix 1997). Fragments of worms were counted as one-half worm (Dickey and Kladivko 1989). We identified earthworms to the level of family for Lumbricidae or genus for native species.

TABLE 1. Characteristics of remnant forests sampled in the Willamette Valley, Oregon, Winter 2000.

Remnant	Size (ha)	Soil Type(s)	% Slope	Dominant Overstory	Dominant Understory
Alderman	12.1	Woodburn silt loam, Woodburn silt clay loam	0-20	Douglas-fir, bigleaf maple	Western swordfern, blackberry, snowberry
Belleview	8.1	clay, silty clay, clay loam	0-10	white oak, red alder	Himalayan blackberry, ivy
Helmick	6.1	loam, clay loam, silty clay loam, sandy clay loam	<5	Douglas-fir, bigleaf maple	Western swordfern, snowberry
Mallard	3.2	McBee silt loam	0	Douglas-fir, white oak	blackberry
Mission Bottom	5.7	silt loam, silty clay loam	20-40	Douglas-fir white oak	Western swordfern, blackberry

Habitat Characteristics

We estimated habitat characteristics at every third sample point and for all points in which we found native earthworms. We estimated basal area of coniferous and deciduous trees >12.5 cm diameter at breast height (dbh), percent of shrub cover (plants >1m in height and <12.5 cm dbh), percent of ground cover (< 1m in height), soil characteristics, and classified sample points into two slope classes: hillside or flat.

Basal area of trees within a 5 m radius of the center of the sample point was estimated from dbh measurements. Shrub cover was estimated separately for woody and herbaceous vegetation (e.g., large ferns) using the line-intercept method (Higgins et al. 1994), with cover recorded at each cardinal direction along a 5 m transect from the sample point. Percent ground cover was estimated by using the quadrat plot method with ocular estimates (Higgins et al. 1994), placing 0.25 m^2 plots 1 m from the sample point at each cardinal direction. Depth of surface organic matter (duff) was measured by inserting a ruler into the layer of organic matter on top of the soil, 1 m from the sample point at each cardinal direction.

Soil samples were collected from the A horizon using a bulk density sampler with a volume of approx. 100 cm^3. Moisture content was calculated after oven-drying 10 g of sample at 105° C for 24 hr. Samples were later air-dried for 3 d at 33° C and sieved (4 mm). Soil aggregates >4 mm, including roots, stones, and sticks, were excluded from all analyses. Percent organic matter was estimated by mass loss on ignition. Each air-dried sample (10 g) was dried in a 100° C oven for 3 hr to obtain the base weight. The sample was then placed in a muffle furnace at 550° C for 5 hr and reweighed. Textural classification (sand and clay content) was estimated by the hydrometer method (Gee and Bauder 1986). Soil pH was estimated in the field using a field dye indicator kit.

Statistical Analyses

We used simple linear regression to estimate the association between abundance of *Toutellus* spp. and lumbricids, given that *Toutellus* were present. Because we were interested in the potential effects of lumbricids on native species, we considered lumbricid counts as the explanatory variable and counts of *Toutellus* as the response variable. We used only sample points in which we located *Toutellus* spp. and thus only the Alderman site was included in analyses. Counts for different dates of sampling were pooled after finding no weather effect. To normalize the distribution of abundance data, counts were square-root transformed prior to analysis.

We used regression analyses to estimate habitat associations. Because the number of *Toutellus* detected were distributed in an almost binary form, we used logistic regression to evaluate habitat characteristics associated with probability that *Toutellus* was present (and detected) in the earthworm samples. We modeled the association of the number of lumbricids detected and habitat characteristics with linear regression. Because of the lack of independence among samples (due to short distance intervals) within a site, we retained site as a covariate in all models. Soil samples were not collected at nine of the *Toutellus* sample points. We excluded these samples when conducting analyses that included soil characteristics in any of the models considered. After finding that soil characteristics were not included in our best models (see Results), we conducted a separate analysis without soil variables in the models considered to allow all sample points with *Toutellus* to be included in the analyses. Analyses were conducted with Proc Logistic and Proc GLM (SAS Institute 1994). We report means and estimated regression coefficients ± 1 SE.

Prior to conducting analyses, we developed 19 (*Toutellus*) to 27 (lumbricids) models of the relationship between habitat and worm abundance (Table 2). Each model allowed us to estimate effects of a different set of habitat characteristics that potentially influenced habitat selection. Evaluation of only the most biologically realistic models reduces the risk of incorrect inference from spurious correlations that often result when many models are evaluated (Burnham and Anderson 1998). Rather than using conventional methods of testing statistical significance of null hypotheses, we used an information-theoretic approach, which ranks models and provides a means of assessing the strength of evidence for one model over another (Burnham and Anderson 1998). The focus of our analysis was to identify the appropriate models for estimating model parameters and their uncertainty (Johnson 1999). We used Akaike's Information Criteria, with small-sample (second-order) bias adjustment (AICc) as the basis for model selection (Burnham and Anderson 1998).

TABLE 2. Comparison of models of the habitat associations of lumbricids and *Toutellus* spp. All five remnant forests were included in analyses of lumbricids and only the Alderman remnant included for *Toutellus*. Sample sizes (n) indicate number of 22 x 22 x 5 cm excavations included in analysis.

				Toutellus spp.[3]			
	Lumbricids[2] (n = 73)			All measurements (n = 25)		Without soil measurements (n = 34)	
Model variables[1]	r^2	ΔAICc[4]	w[5]	ΔAICc[4]	w[5]	ΔAICc[4]	w[5]
pH, org, pH*org, silt, clay, moist, den, basalH, basalC, groundv, wood, shrubW, shrubH, slope	0.35	27.1	0.00				
Above model, without slope	0.35	23.6	0.00				
BasalH, basalC, groundv, shrubW, shrubH	0.19	13.6	0.00				
Basal, groundv, shrubW, shrubH	0.15	14.8	0.00				
BasalH, basalC, groundv, shrub	0.13	16.4	0.00				
Basal, groundv, shrub	0.13	13.8	0.00	5.6	0.01	9.4	0.01
Groundv, shrub	0.12	11.4	0.00	3.4	0.18	6.5	0.01
Groundv	0.11	9.7	0.00	0.9	0.06	4.0	0.04
Basal	0.12	9.5	0.00	1.3	0.05	4.8	0.03
Shrub	0.12	9.0	0.01	2.2	0.03	4.8	0.03
pH, org, pH*org, silt, clay, moist, den	0.26	12.7	0.00				
pH, org, pH*org, clay, moist, den	0.26	10.1	0.00				
pH, org, pH*org, moist	0.24	6.7	0.01				
pH, org, moisture	0.23	4.3	0.04	3.9	0.01	8.2	0.01
pH, org, den	0.23	4.4	0.04	4.5	0.01	9.2	0.01
pH, org	0.22	3.3	0.07	1.9	0.04	6.3	0.01
pH(log), org(log)	0.21	3.7	0.06	1.8	0.04	6.3	0.01
Org(log)	0.21	1.5	0.17	1.1	0.06	4.7	0.03
pH(log)	0.11	9.9	0.00	0.4	0.08	4.0	0.04
Org	0.21	1.0	0.21	1.4	0.05	4.7	0.03
pH	0.11	9.9	0.00	0.3	0.08	4.0	0.04
Moist	0.22	0.0	0.36	2.2	0.03	4.5	0.03
Clay	0.14	7.6	0.01	2.3	0.03		
Den	0.12	9.1	0.01	0.9	0.06	4.6	0.03
Duff	0.12	8.9	0.01	0	0.10	0.3	0.26
Slope	0.11	9.7	0.00	0.5	0.08	0.0	0.31
No effects	0.11	7.4	0.01	0.03	0.10	2.6	0.08

[1] Site (remnant) was included as a categorical covariate in all lumbricid models. Variable acronyms: basalH = basal area of hardwood species, basalC = basal area of coniferous species, basal = basalH + basalC, den = soil density, groundv = ground cover by vegetation, moist = soil moisture, org = organic matter, shrubH = cover of herbaceous "shrubs," shrubW = shrub cover of woody species, shrub = shrubH + shrubW, wood = wood debris ground cover. Models without values were not evaluated for the given taxa.

[2] Includes species within the Lumbricidae.

[3] Soil measurements were not taken on nine sample points. Analyses with n = 25 included soil variables in models whereas analyses with n = 34 excluded soil variables.

[4] Akaike's Information Criteria (with a small sample size correction, AICc) difference between the model with the lowest AICc and the respective model. Lower AICc indicates a better model from which to make inferences.

[5] Akaike's Information Criteria weights (w) estimate the relative likelihood of the given model being the best within the set considered (Burnham and Anderson 1998).

We used AICc weights to compare the relative likelihood of a model being the best (Burnham and Anderson 1998). For the linear regression models we computed AICc with the least-squares method described by Burnham and Anderson (1998). Because at least one model will always be identified as best, we included models that we treated as no-effects models. The model with only

the intercept term served as the no-effects model for *Toutellus;* for lumbricid analyses, the model with only site effects served as the no-effects model.

Results

Vegetative characteristics varied among the five sites, particularly with the relative density of coniferous and deciduous tree species (Table 3). There was little variation of pH and soil density within or among sites. Soil texture varied considerably among sites but there was little within-site variation (Table 3).

We counted a total of 1790.5 earthworms in the five sites (Table 4). Most (97.4%) were lumbricids; we detected 36.5 *Toutellus* and 10 *Argilophilus*. Lumbricids were found in all sites, with percent occurrence ranging from 61.7 to 98.3% of the excavated samples (Table 4). Mean number of lumbricids/sample among sites ranged from 2.8 to 7.8 (6.1 ± 0.41), corresponding to a mean density (individuals/m^2) of 126.3 ± 8.5 (Table 4). Within sites there was high variability in the number of individuals detected (Table 4); a maximum of 21 - 59 individuals/sample were counted among sites. Based on our finding of a mean mass

TABLE 3. Habitat characteristics in remnant forests sampled in the Willamette Valley, Oregon, February–April 2000. Mean and SE were computed from measurements made at sampling points within each remnant.

Habitat Characteristic	Alderman		Belleview		Helmick		Mallard		Mission Bottom	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Conifer stems >12.5 cm dbh (no./ha)	1062.2	151.7	0	0	492.6	230.9	785.8	319.0	341.0	252.4
Deciduous stems >12.5 cm dbh (no./ha)	22.5	0.9	335.1	148.6	479.4	101.1	124.6	83.3	172.2	90.3
Woody shrub cover (%)	63.4	7.2	94.8	2.4	46.4	7.5	31.3	16.2	58.8	11.7
Herbaceous shrub cover (%)	3.1	2.3	0	0	17.9	6.8	20.0	13.3	9.5	9.1
Ground vegetation (%)	74.9	3.6	82.3	4.0	70.1	4.1	89.1	4.2	80.1	5.7
Woody debris cover >10 cm (%)	1.4	1.0	0.9	0.5	3.5	0.9	2.3	1.9	0.4	0.4
Woody debris cover <10 cm (%)	19.2	3.6	8.8	2.1	10.5	2.5	8.6	4.0	18.3	5.4
Bare ground (%)	3.5	1.0	8.0	3.1	15.8	4.3	0	0	1.1	0.6
Duff depth (cm)	4.4	0.6	3.0	0.9	7.6	0.9	4.7	1.7	5.2	0.8
Soil pH	6.0	0.1	6.3	0.1	6.2	0.1	5.9	0.1	6.3	0.1
Soil organic matter (%)	9.4	0.4	12.6	0.9	8.5	0.7	9.1	0.4	8.2	0.3
Sand (%)	16.9	0.5	23.5	2.3	41.6	3.4	23.6	0.9	14.6	0.6
Silt (%)	58.3	0.6	41.1	1.2	31.1	1.7	56.8	0.9	57.9	0.7
Clay (%)	24.8	0.5	35.4	1.5	27.3	2.1	19.6	0.4	27.5	1.0
Moisture content (%)	37.5	1.5	55.9	3.2	38.8	2.0	39.0	2.1	30.4	1.8
Density (g/cm^3)	0.67	0.02	0.62	0.02	0.70	0.02	0.64	0.03	0.71	0.02

TABLE 4. Earthworm abundance in five remnant forests, Willamette Valley, Oregon. Each remnant was sampled twice during February–April 2000.

Remnant	Total no. of sampling point	Lumbricids			*Toutellus*			*Argilophilus*		
		Percent Occurrence[1]	Abundance[2] $\bar{x}$	Abundance[2] SE	Percent Occurrence[1]	Abundance[2] $\bar{x}$	Abundance[2] SE	Percent Occurrence[1]	Abundance[2] $\bar{x}$	Abundance[2] SE
Alderman	61	93.4	6.7	0.79	26.2	0.6	0.18	8.2	0.1	0.04
Belleview	60	98.3	7.0	0.63	0	0	0	0	0	0
Helmick	45	88.9	6.4	1.04	0	0	0	2.2	0.1	0.09
Mallard	60	61.7	2.8	0.52	0	0	0	0	0	0
Mission Bottom	60	88.3	7.8	1.30	0	0	0	0	0	0

[1] Percent of samples (22 x 22 x 5 cm excavation) in which a given taxa was detected.

[2]Mean and SE of the number of earthworms of the given taxa counted in each sample.

of 1.6 g/individual lumbricid, we estimated an average biomass of 1,136 ± 76 kg/ha of lumbricids for the upper soil surface.

In contrast, native species were only found at two sites, with frequencies at these sites ranging from 2.2% to 26.2% (Table 4). Mean number of individuals/sample ranged from 0 to 0.6 (0.16 ± 0.04) among sites, with a maximum number of 8 *Toutellus* and *4 Argilophilus.* Despite the much lower detections of native earthworms than lumbricids, we found a positive association (b= 0.34 ± 0.14; r^2 = 0.33) between lumbricids and *Toutellus* (Figure 1).

Few habitat characteristics that we measured were associated with the abundance of earthworms. Only models of habitat selection that contained variables associated with soil moisture and organic matter were preferable to the no-effects model. For lumbricids these models were twice as likely as the no-effects model to be the best among the set we considered (Table 3). Soil moisture and organic matter were highly correlated (r = 0.81). Counts of lumbricids were positively associated with soil moisture (b= 0.05 ± 0.02) and percent organic matter (b= 0.17 ± 0.06). Presence of *Toutellus* was associated with a similar characteristic, depth of surface organic matter (duff). The model with this single variable was identical in AICc weights to the no-effects model, and not convincingly more likely as the best model compared with other one-variable models that included either soil pH, organic matter, soil density, or slope (Table 3). To further investigate *Toutellus* habitat models, we used all of the sampled areas within the Alderman site, and thus excluded soil texture variables which were not measured at all sample points. From this larger sample, the single-variable model with duff depth and that with slope were the most likely, and were greater than three times more likely than the other models (Table 3). Duff depth tended to be greater at sample points in which we detected *Toutellus* (5.7 ± 1.0 cm) than where they were not detected (3.8 ± 0.4 cm). Of the 34 points sampled for both

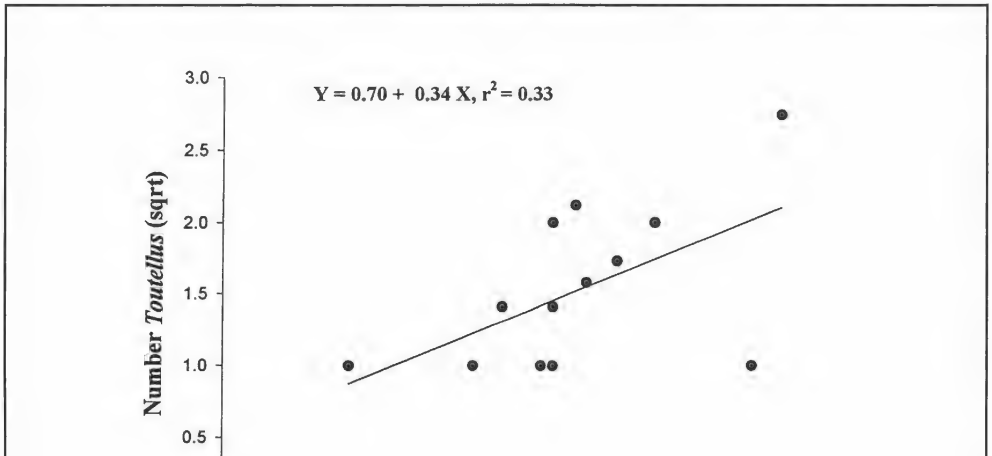

Figure 1. Relationship between the number of *Toutellus* and lumbricid earthworms counted within fourteen 22 x 22 x 5 cm excavations centered on the sampling points within the Alderman site, Willamette Valley, Oregon, February - April 2000. Only excavations within which both lumbricids and *Toutellus* were found were included. Counts were square-root transformed prior to analysis.

earthworms and habitat characteristics in the Alderman site, we detected *Toutellus* in 67.7% (8 of 12) of the sloped sample points and in 27.3% (6 of 22) of those relatively flat. Duff depth was similar between the sloped (4.6 ± 0.5) and flat (4.6 ± 0.7) sample points, demonstrating that the two habitat characteristics associated with the presence of *Toutellus* were not simply correlated with one another.

Discussion

Our results are consistent with previous findings (Kalisz and Dotson 1989, Kalisz and Wood 1995) that introduced lumbricid earthworms are ubiquitous and native species are uncommon in disturbed forests. That we estimated a biomass of >1100 kg/ha of lumbricids from the top 25 cm of the soil surface suggests that they constitute a major component of the animal biomass of these forests. In contrast, native earthworms, comprising two genera (*Toutellus* and *Argilophilus*), were found at only two of five of these remnants and in much lower densities than the lumbricids. Unfortunately, there are no published studies to evaluate abundance of native earthworms in the Willamette Valley prior to the presence of lumbricids.

Contrary to our prediction of a negative effect of introduced taxa on abundance of natives, we found a positive association. As abundance of lumbricids increased, so did abundance of *Toutellus*, suggesting that habitat conducive for introduced earthworms may also be conducive to *Toutellus*. However, because we failed to detect several native species that are presumed to be present in the Willamette Valley, the potential impact of lumbricids on the native earthworm fauna may be great. That we found few individuals of only two native species and high densities of lumbricids in most of the sites warrants further investigation of the potential impact of lumbricids on the native earthworm fauna.

Although native earthworm species may have different ecological requirements from introduced species (Fender 1995) and thus reduce the potential for competition (Kalisz and Wood 1995), little work has been conducted to test hypotheses on these differences. Fender's (1995) work helped form our predictions that native species would predominate in natural forest soils with high clay content, low pH, and along compacted trails, and that native species would be more selective of habitat characteristics than the introduced species of lumbricids. We found no evidence to support these predictions. Habitat variables associated with greater abundance of *Toutellus* were increasing depth of the duff layer and sloped terrain, although effects were weak. Abundance of introduced species (lumbricids) increased as soil moisture and percent organic matter increased, two factors that were highly correlated with each other. These may have been the only factors of statistical importance in our models simply because lumbricids are more likely to be near the surface as soil moisture increases (Edwards and Lofty 1976). We may have failed to detect habitat associations for several of the variables, such as acidity and soil compaction, because of the narrow range of conditions within and among the five sites. Furthermore, that we identified few characteristics associated with earthworm counts may be partially due to increased variation of counts arising from the unknown but likely variable detection rates of earthworms among sample points, sites, and species.

All of our study sites have been fragmented over the past century. Habitat fragmentation often leads to modification of microclimate (Saunders et al. 1991). Blanchart and Julka (1997) noted the possibility that earthworm communities are also affected by the size and shape of habitat patches, and their position in the landscape. Kalisz and Wood (1995) suggested that microclimate, edge effects, influx of introduced taxa, and input of toxic chemicals may reduce the ability of native earthworms to survive or compete with introduced species. Indeed, native species dominated the earthworm fauna in large, undisturbed forests of the southern Appalachians (Kalisz and Dotson 1989). Further work exploring patterns of earthworm diversity and abundance, and landscape factors influencing such patterns would greatly aid our understanding of native and introduced earthworm interactions.

Future research should focus on a broad set of vegetation types to further determine characteristics important to native earthworms in western North America. An experimental approach, coupled with comparative field observations, may be the most fruitful means of understanding the potential impacts of introduced earthworms to the native fauna. Earthworms tend to be clustered (Dickey and Kladivko 1989, Wood and James 1983) and

the likelihood that an individual, although present, may be undetected may be very high for some species. It thus will be important to incorporate estimated detection probabilities into analyses of patterns of earthworm abundance. This, combined with intensive sampling in a broad array of habitats, should increase our knowledge of the impressive diversity of native earthworms, and our ability to evaluate factors that may affect their future existence within highly modified ecosystems.

Acknowledgements

We thank the landowners and managers that allowed us access to the sites: Glen Ford, Scott Hamilton, Vicki Perrett, Bill and Susan Usrey, and Rob Westberg. We are grateful to Jeff Rosier for locating sites; to Cheron Ferland, Jason Adams, Autumn Bauwens, Kale Haggard, and Stephanie Lamb for their dedication in conducting field work; to Will Austin and the Central Analytical Laboratory (Dept. of Crop and Soil Science, Oregon State Univ.) for assistance with soil analyses; to Jim Kagan and the Oregon Natural Heritage program for collaboration and assistance with identifying potential study sites; and to Mary Fauci and Stewart Wuest for helpful reviews of earlier drafts of this manuscript. This work was made possible by funds provided by the Biological Resources Division of the U.S. Geological Survey, the U. S. Fish and Wildlife Service, and through collaborative agreements with the Oregon Cooperative Fish and Wildlife Research Unit. Cooperators of the Unit included the U. S. Fish and Wildlife Service, Oregon State University, Oregon Department of Fish and Wildlife, the Wildlife Management Institute, and the Biological Resources Division of the U. S. Geological Survey. Publication of this paper was supported, in part, by the Thomas G. Scott Publication Fund.

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Received 17 May 2001
Accepted for publication 10 September 2001

Gary L. Larson, United States Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331

and

Robert L. Hoffman,[1] College of Oceanic and Atmospheric Sciences, Oregon State University, 3200 SW Jefferson Way, Corvallis, Oregon 97331

Abundances of Northwestern Salamander Larvae in Montane Lakes With and Without Fish, Mount Rainier National Park, Washington

Abstract

In Mount Rainier National Park, the northwestern salamander usually inhabits relatively large and deep lakes and ponds (average size = 0.3 ha; average depth > 2 m) that contain flocculent, organic bottom sediments and abundant coarse wood. Prior to 1970, salmonids were introduced into many of the park's lakes and ponds that were typical habitat of the northwestern salamander. The objective of this study was to compare, in lakes and ponds with suitable habitat characteristics for northwestern salamanders, the observed abundances of larvae in lakes and ponds with and without these introduced salmonids. Day surveys of 61 lakes were conducted between 1993 and 1999. Fish were limited to lakes and ponds deeper than 2 m. For the 48 lakes and ponds deeper than 2 m (i.e., 25 fishless lakes and 23 fish lakes), the mean and median observed abundances of northwestern salamander larvae in fishless lakes and ponds was significantly greater than the mean and median observed abundances of larvae in lakes and ponds with fish. Northwestern salamander larvae were not observed in 11 fish lakes. These lakes were similar in median elevation, surface area, and maximum depth to the fishless lakes. The 12 fish lakes with observed larvae were significantly lower in median elevation, larger in median surface area, and deeper in median maximum depth than the fishless lakes. Low to null observed abundances of northwestern salamander larvae in lakes and ponds with fish were attributed to a combination of fish predation of larvae and changes in larval behavior.

Introduction

Salamander larvae are the top native aquatic vertebrate predators in many lakes and ponds in the Cascade Range of the Pacific Northwest (Taylor 1983; Tyler et al. 1998a). The two dominant taxa in the Cascades of Washington State are the long-toed salamander (*Ambystoma macrodactylum* Baird) and the northwestern salamander (*Ambystoma gracile* [Baird])(Nussbaum et al. 1983). At North Cascades National Park Service Complex (NOCA) in northern Washington, only the long-toed salamander is present east of the hydrological divide of the Cascade Range. Long-toed salamander larvae occupy a wide variety of habitats ranging from shallow ephemeral ponds to deep lakes (Tyler et al. 1998a). Although both species are present on the west side of the divide, distribution of the northwestern salamander in NOCA is more restricted than the long-toed salamander (Nussbaum et al. 1983) and limited to the deeper lakes and ponds. On the west slope, the long-toed salamander appears to be absent from lakes and ponds inhabited by the northwestern salamander (Liss et al. 1995). Compared to fishless systems, observed abundances of long-toed salamander and northwestern salamander larvae are reduced in lakes and ponds inhabited by introduced fish in NOCA (Liss et al. 1995; Tyler 1998a).

About 150 km south of NOCA, long-toed salamanders and northwestern salamanders are widely distributed in Mount Rainier National Park (MORA). The species are seldom sympatric (Brokes 2000). The long-toed salamander inhabits small, shallow ponds (mean size = 0.08 ha; mean depth = 0.6 m) with muddy or consolidated bottom sediments (Brokes 2000). The northwestern salamander typically inhabits larger, deeper systems (mean size = 0.3 ha; mean depth > 2 m) than does the long-toed salamander, and these systems have flocculent, organic bottom sediments and abundant coarse wood (Brokes 2000).

Reproducing populations of introduced salmonids, which were stocked prior to 1970, inhabit 27 of the deeper lentic systems at MORA (Barbara Samora, Mount Rainier National Park, personal communication). Thus, in MORA

[1]Author to whom correspondence should be addressed. E-mail: robert.hoffman@orst.edu

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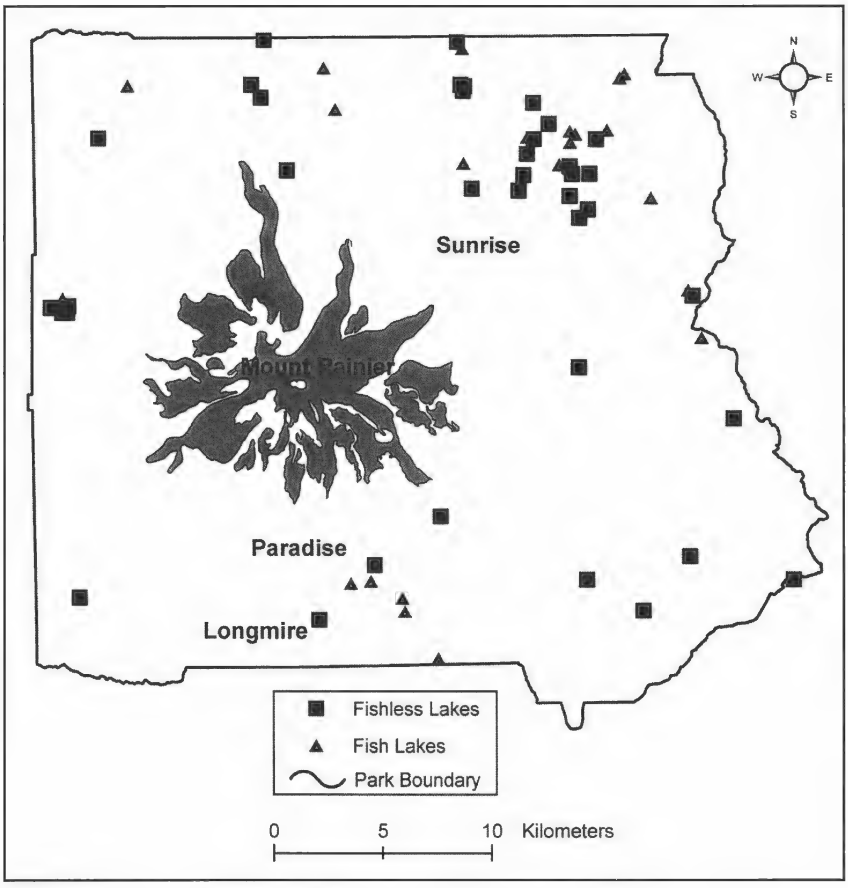

Figure 1. Location of 61 survey lakes in Mount Rainier National Park, Washington.

northwestern salamander larvae likely interact more with introduced fish than do long-toed salamander larvae. The objectives of this study were: 1) compare the observed abundances of northwestern salamander larvae in lentic systems with and without reproducing populations of introduced salmonids; and 2) determine if introduced salmonids have affected larval populations of the northwestern salamander.

Study Area

Mount Rainier National Park is located on the western slopes of the Cascade Range in south-central Washington State (Figure 1). Mount Rainier (4393 m) dominates the 969 km^2 park. The rugged, mountainous, volcanic terrain has a diversity of climatic and geologic conditions, soils, and vegetation. Annual precipitation is ~ 150 cm at the lower elevations and > 250 cm at higher elevations. More than 75% of the precipitation falls as snow between October and March (Richardson 1972). Park lakes are covered with deep snow and granular ice in winter (Larson et al. 1994). The open-water season for lakes and ponds generally begins in late June to early July and lasts until October-November.

From 1993 through 1999, we surveyed 61 montane lakes and ponds across the landscape of MORA (Table 1; Figure 1) to document the observed abundances of northwestern salamander larvae in lentic systems with and without fish (Table 1). The presence of fish in a lake or pond was

TABLE 1. Physical attributes and larval salamander counts (number per 100 m) in 61 lakes, Mount Rainier National Park (MORA).

Parameter	Fishless Lakes	Fish Lakes
Number of lakes:	38	23
sampled in one year	32	17
sampled multiple years	6	6
Elevation (m):		
range	670–1772	974–1784
mean	1561	1493
median	1591	1492
Surface area (ha):		
range	0.05–5.32	0.11–7.33
mean	0.94	2.99
median	0.69	2.60
Maximum depth (m):		
range	0.4–20.0	2.6–29.0
mean	4.2	10.0
median	2.5	8.5
Larval counts:		
range	1.6–395.0	0–27.6
mean	76.8	6.4
median	58.1	0.3

TABLE 2. Variation of larval salamander counts (number per 100 m) in lakes surveyed in multiple years. Larvae were observed in all six fishless lakes and in only two of six fish lakes sampled in multiple years.

Lake	Fish Status	Years Sampled	Number	Annual Mean
LM23	Fishless	1996	94.3	
		1999	45.3	69.8
LM26	Fishless	1996	4.4	
		1999	79.3	41.8
LM30	Fishless	1996	42.5	
		1999	130.0	86.2
LM32	Fishless	1996	101.3	
		1999	11.3	56.3
LO26	Fishless	1997	69.1	
		1998	14.6	41.8
LZ31	Fishless	1996	13.3	
		1999	136.8	75.1
LC01	Fish	1997	5.1	
		1999	6.1	5.6
LM17	Fish	1996	0	
		1999	1.3	0.6

determined either by direct observation of fish or, when the presence of fish was not obvious, through the use of gillnets set for several hours during a survey visit.

Methods

Forty-nine of the lakes and ponds in this study were sampled once from late July to early September between 1993 and 1999 (Table 1). Counts of salamander larvae for these lakes or ponds were extrapolated to the number of larvae observed per 100 m. Observed larval abundances for the 12 lakes and ponds sampled in multiple years (Table 1) are averages of the extrapolated counts for all survey years (Table 2). Larval counts in a lake can vary considerably from year to year. Therefore, counts based on averaging multiple year surveys may not adequately represent this variability (Table 2). Only lakes and ponds with habitat characteristics determined to be typical of MORA systems inhabited by northwestern salamander larvae, especially lakes and ponds with flocculent, organic bottom sediments, were included in this study.

We determined species distributions and the observed abundances of salamander larvae by visual encounter and snorkeling surveys (Thoms et al. 1997; Tyler et al. 1998a; Brokes 2000). Although care was taken to use each method as efficiently and effectively as possible, each survey method may have underestimated the actual abundances of larvae in the survey lakes or ponds. Therefore, larval counts were considered to represent the observed rather than actual relative abundance of salamander larvae in each system. Visual encounter surveys were used in two ponds that were too shallow to snorkel (<0.7 m) (Brokes 2000). These surveys were performed according to protocol described by Thoms et al. (1997), and involved searching for salamander larvae while slowly walking/wading the shoreline and nearshore area of each pond. Snorkel surveys were accomplished by swimming transects parallel to the lake or pond shoreline, recording larvae observed within a band extending from the shoreline to 2 m offshore.

Number Cruncher Statistical System 2000 (NCSS 2000) was used for all statistical analyses (Hintze 1998). Lakes were grouped according to the presence or absence of fish and maximum depth (i.e., < 2 m or ≥ 2 m). All lakes occupied by fish were ≥ 2 m in maximum depth since fish were typically introduced into deeper mountain lakes where they could survive winter lake conditions at high-elevation (Bahls 1992). Fishless lakes were grouped into lakes < 2 m and lakes ≥ 2 m maximum

depth. The grouping of fishless lakes into two depth categories was done so that the observed abundances of salamander larvae in fish lakes could be compared to the observed abundances in fishless lakes that were deep enough (i.e., ≥2 m) for fish survival if fish were to be introduced into these systems. One-way ANOVA (Hintze 1998) was used to compare the mean number of larvae observed per 100 m in fishless lakes ≥2 m maximum depth (n = 25) and fish lakes (n = 23). Kruskal-Wallis One-way ANOVA on Ranks (Hintze 1998) was used to compare the median number of larvae observed per 100 m in the fishless lakes ≥ 2 m maximum depth and the fish lakes. These tests were also used to compare the observed abundances of larvae in fishless lakes < 2 m (n = 13) with fishless lakes ≥2 m maximum depth. The level of significance for each analysis was P = 0.05. Kruskal-Wallis One-way ANOVA on Ranks (Hintze 1998) was also used to compare the median physical attributes of elevation, surface area, and maximum depth of the fishless lakes ≥ 2 m maximum depth with fish lakes with observed salamander larvae (n = 12) and fish lakes without observed salamander larvae (n = 11). The level of significance for these comparisons was Bonferroni adjusted to P = 0.025.

Results

Day surveys of 61 lakes at MORA indicated that the observed abundances of northwestern salamander larvae differed significantly between fishless lakes and lakes with fish (Table 1; Figure 2). The mean number of larvae observed in all fishless lakes (n = 38) was 12 times greater than in all fish lakes (n = 23), and the median number of larvae observed in fishless lakes was quite large compared to the median number observed in lakes with fish (Table 1). Salamander larvae were observed in all fishless lakes surveyed, whereas of the 23 fish lakes surveyed, larvae were observed in 12 (52%) of the lakes.

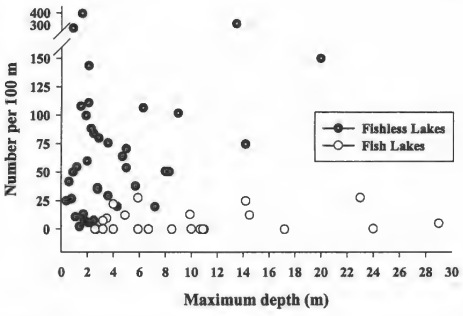

Figure 2. Observed abundances of northwestern salamander larvae in survey lakes of different depths and fish status, Mount Rainier National Park.

The mean and median numbers of northwestern salamander larvae observed in the 25 fishless lakes ≥2 m maximum depth were significantly greater than the mean and median numbers of larvae observed in the fish lakes (mean: F-ratio = 25.52, P < 0.001; median: χ^2 = 28.4, P < 0.001; Table 3). Abundances of ≥ 50 larvae per 100 m were observed in 16 (64%) of the fishless lakes ≥ 2 m maximum depth, and there were over 100 larvae per 100 m observed in six of these lakes. The highest number of larvae observed in the fish lakes was 27.6 per 100 m and this observed abundance was 11.5 times lower than the maximum observed abundance for the fishless lakes ≥ 2 m maximum depth. There were no significant differences in the mean and median numbers of larvae observed between the two categories of fishless lakes (Table 3).

TABLE 3. Larval salamander counts (number per 100 m) in fishless and fish survey lakes. Maximum depth is labeled Zmax, and asterisk signifies significant difference with fishless lakes. ≥2 m maximum depth.

	Lake Status		
	Fishless		Fish
	< 2 m Zmax	≥2 m Zmax	All Lakes
Number of lakes	13	25	23
Mean	78.9	75.7	6.4*
Median	41.8	69.8	0.3*
Range	1.6–395.0	5.8–314.4	0–27.6

The physical attributes of survey lakes differed when compared by lake group. On average, the fishless lakes were higher in elevation, smaller in surface area, and shallower in maximum depth than the fish lakes (Table 1). These differences were significant between fishless lakes ≥2 m maximum depth (n = 25) and fish lakes in which salamander larvae were observed (n = 12). The fish lakes with observed salamander larvae were lower in median elevation (χ^2 = 5.84, P = 0.02), larger in median surface area (χ^2 = 7.16, P = 0.007), and deeper in median maximum depth (χ^2 = 6.66, P = 0.01) than the fishless lakes ≥2 m maximum depth (Table 4). These attributes did not differ

significantly between the 11 fish lakes with no observed larvae and fishless lakes ≥2 m maximum depth (Table 4).

TABLE 4. Median physical attributes of survey lakes. Maximum depth is labeled Zmax, and asterisk signifies significant difference with fishless lakes ≥2 m maximum depth.

	Lake Status		
	Fishless	Fish	
Attribute	≥2 m Zmax	with larvae	without larvae
Number of lakes	25	12	11
Elevation (m)	1654	1478*	1617
Surface Area (ha)	0.92	2.99*	2.12
Maximum depth (m)	4.3	9.9*	6.7

Discussion

Northwestern salamander larvae were not readily observed in lakes containing fish and we conclude that the observed abundances of larvae were significantly lower in fish lakes compared to fishless lakes (Table 3; Figure 2). Similar conclusions were reached in other studies of the observed abundances of northwestern salamander larvae in lakes with and without fish (Sprules 1974; Taylor 1983). In fact, no larvae were observed in 11 (48%) of the MORA lakes with fish, which suggests that fish either eliminated larvae from the lakes or larvae were extremely difficult to detect. These lakes were similar in elevation, size, and depth to fishless lakes ≥2 m maximum depth where salamander larvae were typically observed. Conversely, salamander larvae were observed in 12 fish lakes which were significantly lower in elevation, larger in surface area, and deeper in maximum depth than fishless lakes ≥2 m maximum depth. This result indicates that northwestern salamander larvae are able to co-exist with introduced fish in these larger and deeper systems.

We do not know, however, how representative these observed abundance estimates were of the actual size of the populations that were studied. In lakes and ponds with fish, estimates of northwestern salamander numbers can be low because larvae generally become less active and are capable of altering their diel pattern of behavior and habitat utilization in an effort to reduce exposure to predation (Efford and Mathias 1969; Sih 1987). Reducing exposure to fish predation may take the form of increased use of refugia such as coarse woody debris, rock talus, and aquatic vegetation (Taylor 1983; Tyler et al. 1998b), which would reduce the visibility of salamander larvae to snorkelers. Northwestern salamander larvae also tend to be nocturnal in lakes and ponds that contain fish (Efford and Mathias 1969; Sprules 1974; Taylor 1983; Tyler et al. 1998a). In fact, the numbers of northwestern salamander larvae were 10 times higher at night than were counts obtained during day surveys in a NOCA lake with fish (Liss et al. 1995). Therefore, we conclude that the lower observed abundances of northwestern salamander larvae that we detected in MORA lakes with fish were due, in part, to a combination of direct fish predation on larvae and changes in larval behavior to avoid fish predation.

Northwestern salamander larvae were not typically associated with shallow ponds (i.e., < 2 m maximum depth) at MORA when the ponds were either ephemeral or when the composition of the bottom substrate was firm and inorganic (Brokes 2000). The shallow ponds inhabited by the larvae in this study had soft, organic bottom substrates. Introduced salmonids do not typically survive in ponds < 2 m depth. Thus, these shallow systems provided an additional refuge for northwestern salamander larvae from fish predation. Nonetheless, across the landscape of MORA, northwestern salamander larvae were able to persist in over 50% of the lakes with introduced salmonids.

The relationships between introduced fish and salamander larvae were different between MORA and NOCA, which raises some interesting management issues. At MORA, only northwestern salamander larvae were impacted by fish, although the present distribution of long-toed salamanders in MORA lentic systems could reflect past fish stocking patterns in park lakes. Larvae of both northwestern and long-toed salamanders were impacted by introduced salmonids at NOCA (Liss et al. 1995; Tyler et al. 1998a). Yet, in both parks the interaction between fish and salamander larvae was mostly related to the distributions of the two salamander species in the Pacific Northwest (Nussbaum et al. 1983) and their interspecific interactions (Hoffman and Larson 1999). Northwestern salamanders and long-toed salamanders have overlapping distributions at the landscape level at MORA, which is on the west side of the hydrological divide of the Cascade Range. In MORA, northwestern salamander larvae inhabit large, deep, permanent lakes in which fish can

survive, whereas long-toed salamander larvae are restricted to small, shallow, semi-permanent to permanent systems uninhabitable by fish (Brokes 2000). In NOCA, the northwestern salamander occurs only on the west side of the hydrological divide where its distribution is limited, whereas the long-toed salamander is widely distributed on both sides of the divide. For this reason, long-toed salamander larvae were able to inhabit larger and deeper lakes on the east side of NOCA that would have been occupied by northwestern salamander larvae at MORA. This pattern of salamander species distribution was a factor in the impact of both species by introduced fish at the landscape level at NOCA. These results suggest that natural resource managers should be careful about transposing research information from one location to another.

Acknowledgements

We thank Barbara Samora, Mount Rainier National Park resource management specialist, for her ongoing support of this project. We also thank Brendan Brokes and his field crews for collecting the data. Financial support was provided by Mount Rainier National Park (Tahoma Woods, Star Route, Ashford, WA 98304) and the USGS Forest and Rangeland Ecosystem Science Center (3200 SW Jefferson Way, Corvallis, OR 97331).

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Received 14 May 2001
Accepted for publication 3 September 2001

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Adam Moles[1] and **Ryan Scott,** Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau, Alaska 99801-8626

Growth and Behavior of Juvenile Alaskan Flatfishes in the Laboratory

Abstract

Juvenile Pacific halibut reared in the laboratory grew at a faster rate and had a more uniform distribution in behavior tests than juveniles of yellowfin sole and rock sole. Juvenile yellowfin sole and rock sole had similar 90-d growth rates (0.71-0.83% BWD) in the laboratory at 10°C, whereas Pacific halibut grew significantly faster (1.29% BWD). Rock sole grew the same on both mud and sand, despite a known preference for sand substrate in the field. Yellowfin sole and rock sole had an aggregated distribution in the tanks as measured by nearest-neighbor analysis regardless of the presence of other species, whereas Pacific halibut had a uniform distribution. These are the first observations of growth and behavior of juveniles of these species in the laboratory.

Introduction

Understanding interspecific differences in growth and behavior among various species of juvenile flatfishes may increase understanding of such specific differences as time spent in nursery areas, vulnerability to predators, types and sizes of prey items, intraspecific and interspecific competition for food and space, and productivity of the stock. These processes are all influenced to some degree by initial growth (Weatherley and Gill 1987) and social interactions (Olla et al. 1996) of juveniles of many fish species. Growth also hastens or delays recruitment of flatfishes into the fishery: larger age-0 flatfishes have reduced predation and faster maturation than smaller age-0 flatfishes (van der Veer et al. 1994). In addition, behavior can regulate distribution, feeding, and predator avoidance in many fish species (Olla et al. 1996).

Intuitively, different species may have different growth rates and distributions as mechanisms for partitioning the nursery grounds. Juvenile flatfishes reduce competitive interactions between species through differences in habitat, such as depth and substrate (Norcross et al. 1995). These differences in field distribution of similar-sized individuals are probably the result of a complex interaction of a number of variables such as interspecific differences in growth rates and behavioral interactions.

1 Author to whom correspondence should be addressed. Email: Adam.Moles@noaa.gov

To better understand these initial differences among species of Pacific flatfishes, we assessed growth rates and spatial distribution among newly settled recruits of three commercially important species of flatfishes. We chose young-of-the-year Pacific halibut (*Hippoglossus stenolepis*), yellowfin sole (*Limanda asper*), and rock sole (*Lepidopsetta bilineatus*). The adults of these species constitute over half of the flatfish catch in the northeastern Pacific Ocean, totaling a high of nearly 300,000 metric tons in 1992 (FAO 1995). The combined flatfish fishery is the third largest fishery in the northeastern Pacific Ocean, after walleye pollock (*Theragra chalcogramma)* and Pacific salmon (*Oncorhynchus* spp.) (FAO 1995). Extensive knowledge has been gathered about adults of these flatfish species, but far less is known about the juvenile stage. Because many of the environmental conditions that affect growth and behavior cannot be controlled in the field, our studies were conducted in the laboratory.

Following a planktonic larval stage, the recruits of all three species settle out into subtidal nursery areas (<40 m deep) for the first year or two (Norcross et al. 1995) where they feed largely on crustaceans. Following migration into deeper waters as adults, the Pacific halibut grow to nearly 3 m in length, whereas yellowfin and rock sole are typically <45-55cm. In the study described here, we compared growth rates and spatial distributions among young-of-the-year flatfish juveniles to determine whether differences were evident as early as the first year of life.

Methods

Preparation of Animals

Yellowfin sole and rock sole were obtained from Auke Bay, Alaska, by 6-mm-mesh beach seine in June, 1994 and 1995. Pacific halibut were collected in 10–30 m depths in Middle and Kalsin Bays off Kodiak Island by plumb-staff beam trawl (4-mm mesh) in August 1994 and 1995. All specimens (46–109 mm standard length, mean 69 mm ± 15.9) were transported live to the Auke Bay Laboratory and held in flowthrough seawater tanks on a mixed sand and mud substrate. Fish were held for two months to acclimate to laboratory conditions.

Individual fish were identified for repeated size measurements and behavioral observations by marking juveniles on the ventral surface at one or more of four locations along the lateral margin with Alcian Blue dye (65 mg/mL aqueous solution) to give each fish a unique mark. This allowed us to measure the growth rates in each fish rather than following the mean change of a group of fish. This dye marking method (Thedinga and Johnson 1995) is a fast, external, non-invasive procedure that permits mark retention even in rapidly growing juvenile fishes. Unanesthetized flatfish were jet injected with dye using a Panjet held 25 mm above the skin surface. Excess dye was wiped off, and the fish held in a recovery tank for 1 hr to verify dye retention. Alcian Blue dye does not affect juvenile flatfish growth, alter tissue structure, or become incorporated into internal organs (Thedinga et al. 1997).

Growth Tests

Growth tests were conducted in 70-L tanks (30 x 60 x 40 cm) under outdoor translucent panels with a constant 12 hr/d of supplemental full-spectrum lighting. Seawater flow rates were 1.4 L/m at 28‰ salinity and 10°C, such as is commonly observed during late summer in flatfish nursery areas in southeastern and southcentral Alaska. Temperature was controlled by resistive heaters, mercury switches, and associated relays.

Groups of fish were reared on specific substrates. Each species was tested on its preferred sediment, Pacific halibut and rock sole on sand, yellowfin sole on mud (Moles and Norcross 1995). In addition, rock sole was also tested on mud so that growth for that species could be measured on preferred and unpreferred sediments. Mud was gathered intertidally, frozen and thawed three times to kill any organisms present, then sieved to remove particles and macrofaunal prey items organisms larger than 63 µm. Sand (64–249 µm diameter) obtained from a local gravel yard was sieved to yield a mean particle size of 125 µm. Fish were fed to satiation with a daily ration of commercial blood worms (*Tubifex tubifex*) and mysids (*Mysis* spp.) for two weeks before and throughout the test. Crustaceans such as mysids are a common component of juvenile flatfish diets, and the addition of the bloodworms enhanced the feeding response. The fish were fed six times per day to reduce feed waste and size variance due to possible competition for food among fish (Brännäs and Alanärä 1993). All fish ate voraciously when food became available.

There were four treatment groups (Pacific halibut on sand, yellowfin sole on mud, rock sole on sand, and rock sole on mud), each with 20 fish, reared for 90 d. Because it was only possible to obtain 10 distinctive dye marks, it was necessary to spread the 20 test fish of each treatment among two tanks. This gave a final total of 8 tanks of 10 fish each.

Individual lengths (to nearest mm) and weights (in mg) were measured at 0, 30, 60, and 90 d on the same individually-marked fish. Fish were weighed live in a tared beaker of water, then quickly measured for length and returned to the water. Growth rates for length (incremental growth rate) and weight (specific growth rate) were calculated for each fish (Fonds et al. 1995). Daily length increments (dL) were computed from differences in standard length (L) over time as: $dL = (L_{end} - L_{start})/t$, where t is time in days. Specific growth rate was computed as: $G = (\ln W_{end} - \ln W_{start})/t \times 100$, where W is body wet weight. Only the 90 d growth rates are presented here. Differences in growth rates between the four treatment groups were analyzed using a repeated measures one-way ANOVA at day 0 and day 90 followed by Tukey's test of multiple comparisons at $P = 0.05$.

Spatial Behavior Tests

The spatial distribution of flatfishes was determined using a grid painted on the bottom of a 4.8-m diameter 18,000 L circular tank divided into 118 observation areas. Water depth was 1 m, flow rate 20 L/min (to maintain sufficient oxy-

TABLE 1. Mean lengths, weights, and growth rates (±SE) of three species of juvenile flatfishes reared in the laboratory for 90 d. IGR= incremental growth rate as mm increase per day, SGR= specific growth rate as % body weight per day, N= 20. Within IGR or SGR, means with the same superscript are not significantly different (P<0.05).

	Halibut		Yellowfin sole		Rock sole on mud		Rock sole on sand	
	0 d	90 d	0 d	90 d	0 d	90 d	0 d	90
Length (mm)	72 (1.6)	93 (1.4)	71 (4)	89 (4)	66 (4)	79(4)	67 (4.1)	84 (3.9)
Weight (g)	4.10 (0.29)	11.63 (0.62)	4.38 (0.77)	8.89 (1.4)	3.76 (0.79)	6.2 (0.94)	3.96 (0.85)	6.9 (0.92)
IGR		0.24(0.01)[a]		0.19 (0.01)[b]		0.15 (0.01)[b]		0.19 (0.01)[b]
SGR		1.29 (0.03)[a]		0.83 (0.04)[b]		0.71 (0.01) [b]		0.82 (0.10)[b]

gen), salinity 29‰, and temperature 10°C; no sediment was present. Twenty Alcian blue dye-marked juveniles (average length 80 mm) of the test species and 20 unmarked fish of the same or a different species were chosen randomly and introduced to the tank by net. Using the grid, we measured the distance between each marked fish and its marked nearest neighbor at 30 min intervals for 20 hr, allowing us to calculate mean nearest neighbor ratios over 20 hr periods for each group. After 20 hr, the fish were removed and 40 new fish of the next trial were introduced. All 6 combinations (halibut/halibut, yellowfin sole/yellowfin sole, rock sole/rock sole, halibut/yellowfin, halibut/rock sole, and yellowfin sole/rock sole) were tested with five replicate trials each for a total of 100 test individuals per species. No fish was used for more than a single trial to insure independent observations.

The distance-to-nearest neighbor method (Clark and Evans 1954) described the intraspecific spatial distribution of a given species in the presence of other flatfishes, both of the same and of another species. Nearest-neighbor distances were calculated between marked individuals of the same species, but not of different species. The measure of spacing (R) indicates the degree to which the distribution of the sample deviates from a random distribution (R = 1). The smaller the value of R, the more aggregated the distribution; the higher the value, the more uniform the distribution. We examined differences in nearest neighbor ratios using Wilcoxon signed rank tests.

Results

All fish grew substantially over the 90-d test period. Yellowfin sole weights increased 103%, rock sole weights increased 65% (mud) and 74% (sand), and halibut weights increased 184%. Differences in initial size between the species were not significant for length or weight. Initial mean condition factors also did not differ significantly among all tanks and treatment groups.

Pacific halibut grew significantly faster than the other treatment groups ($P < 0.001$). Daily incremental growth rates (mm/d) were significantly greater ($P < 0.05$) for Pacific halibut than for rock sole or yellowfin sole (Table 1). By day 90, Pacific halibut had grown 0.24 mm/d, 26% greater than rock sole on sand or yellowfin sole. All of these treatment groups increased in length greater than rock sole on mud. There was a significant difference in incremental growth rate but not in specific growth rate between rock sole on mud and on sand. Other differences in growth rate between species or substrate types were not significant. Yellowfin sole and rock sole grew at nearly identical rates throughout the experiment .

During the behavior tests, halibut distributed themselves uniformly R = 1.83-2.00) in the experimental tanks when other species were not present. In contrast, when all 40 fish in the tank were yellowfin sole, more aggregation occurred ($R = 0.86 \pm 0.02$). Rock sole were significantly ($P < 0.001$) more aggregated ($R = 0.71 \pm 0.01$) than yellowfin sole. Distribution patterns for each species did not change when a second species was present (Table 2), except for a decrease in uniformity of Pacific halibut when rock sole were present. Both yellowfin sole and rock sole became slightly

TABLE 2. Nearest-neighbor distances (R values ± SE) for experimental groups of marked juvenile flatfishes of the same species (measured species) in the presence of an equal sized group of the same or a different species (influence species). N= 100 fish.

	Influence Species		
Measured Species	Yellowfin sole	Rock sole	Pacific halibut
Yellowfin sole	0.86 (0.01)	0.66 (0.01)	2.00 (0.3)
Rock sole	0.79 (0.01)	0.71 (.01)	1.83 (0.02)
Pacific halibut	0.83 (0.01)	0.73 (0.01)	1.94 (0.02)

more aggregated in the presence of the other species, but this difference was significant only for yellowfin sole ($P < 0.01$). The distribution of Pacific halibut was not significantly different in the presence of yellowfin sole, but was significantly less uniform in the presence of rock sole ($P < 0.01$). Yellowfin sole and rock sole did not alter their spacing in the presence of Pacific halibut.

Discussion

This is the first laboratory estimate of growth rates following settlement for these valuable commercial species, a period that is important to subsequent survival. Flatfishes, as most fishes, grow most rapidly as juveniles (Paul et al. 1994), and any reduction in juvenile growth rate prolongs the juvenile stage. Mortality during this phase and timing of onset of maturation are directly determined by fish size (Zijlstra et al. 1982, Rijnsdorp 1993). As fish size increases, predation on the fish is reduced for some flatfishes, and in such cases survival is related directly to growth (Witting and Able 1993, van der Veer et al. 1994). Fish that are able to grow quickly during the early juvenile stage, such as Pacific halibut, are less susceptible to predation and have a competitive advantage over slower-growing fish.

The differences in growth between Pacific halibut and the other flatfish species examined in this study are interesting, given the unique energy requirements of Pacific halibut. Pacific halibut, which grew more rapidly than yellowfin sole or rock sole in our study, have greater energy expenditures than yellowfin sole. The oxygen requirement for juvenile halibut is four times higher than for yellowfin sole, due to longer migrations and more active feeding (Paul et al. 1994). Juvenile halibut compensate for this high rate by eating relatively larger meals than do adult fish (Paul et al. 1994). In our study, growth rates of Pacific halibut estimated by length were 26% greater than for yellowfin sole, and the specific growth rate of halibut over the 90 d test period was 55% greater than for yellowfin sole. The growth rates of flatfish in our study are similar to estimates of growth in the first year using age and size data from the Gulf of Alaska. Smith et al. (1995) estimated that yellowfin sole in the Gulf of Alaska grow 0.5% BWD in their first year and Paul et al. (1994) estimated that Pacific halibut growth is at least 0.75% BWD. Pacific halibut juveniles grow rapidly, tripling in length by age-1 (Southward 1967). This initial surge of growth is an important factor in determining year class strength in Pacific halibut (Hagen and Quinn 1991).

Despite strong evidence from both laboratory and field studies that rock sole have a preference for sand over mud, the growth rates for rock sole on sand were not significantly greater than rock sole on mud. When given a choice in the laboratory between a variety of substrates, juvenile rock sole select those substrates containing sand nearly every time. When given a choice between mud and sand only, rock sole always selected sand (Moles and Norcross 1995). In the field, juvenile rock sole are often found on sand substrates (Norcross et al. 1995).

Pacific halibut not only differ from the other two species in spatial behavior, but also have different feeding behavior and they engage in territorial partitioning. Pleuronectids rely on visual cues in diurnal feeding (de Groot 1971) in addition to various levels of chemoreception. In our tests, Pacific halibut fed in the water column and relied heavily on visual detection of prey. Adult Pacific halibut maintain home areas spatially distinct from the home areas of other Pacific halibut (Phillip Hooge, U.S. Fish and Wildlife Service, Glacier Bay, Alaska, personal communication). This is similar to the uniform distribution of the juvenile Pacific halibut in our study. In contrast, the demersally feeding yellowfin sole and rock sole may aggregate for the same reason other species school, such as protection from predators.

Female Pacific halibut reach an adult length of 1 m within only 8 yr (Trumble et al. 1993) in contrast to yellowfin sole, which mature at an average length of 28 cm about 9 yr (Wilderbuer et al. 1992). Rock sole are believed to have a similar age and size at 50% maturity as yellowfin sole. This tremendous difference in growth was evident even in the young-of-the-year in our study. Significantly greater growth rates as age-0 juveniles would allow Pacific halibut to move offshore sooner, escape nearshore predators at an earlier age, and mature quickly. Additionally, when Pacific halibut distribute themselves uniformly with respect to each other, competition is reduced and territory is partitioned. Rather than adopt agonistic behavior common to such fish as salmonids (Ryer and Olla 1995) to compete for food, Pacific halibut may establish hunting areas devoid of other

Pacific halibut. The idea that some of the differences in size and distribution of adult flatfishes are the result of differences in growth and behavior of age-0 juveniles deserves additional study in the field.

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Received 9 April 2001
Accepted for publication 28 August 2001

Acknowledgements

The authors would like to thank Dr. Brenda Norcross of the University of Alaska Fairbanks for her reviews, advice, and encouragement in the execution of this study.

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John F. Lehmkuhl,[1] USDA Forest Service, Pacific Northwest Research Station, 1133 N. Western Avenue, Wenatchee, Washington 98801

The Effects of Spring Burning and Grass Seeding in Forest Clearcuts on Native Plants and Conifer Seedlings in Coastal Washington

Abstract

Seeding clearcuts with grasses and legumes is used to increase ungulate forage, reduce browsing on seedlings, reduce competition with seedlings, or control erosion, but, the effects on native plants and conifer seedlings are poorly known. Also, a shift to spring or no burning of clearcuts may alter the effectiveness of seeding and interactions with native species and conifer seedlings. I quantified over 5 yr the effects of burning (none, spring) and forage grass seeding (0, 22, or 44 kg/ha seed, plus fertilizer) on seeded forage production, native and exotic plant cover and richness, and the survival and growth of planted conifer seedlings on two clearcuts in coastal forest of western Washington. Burning doubled production of seeded grass, but seeding rate (22kg/ha vs. 44 kg/ha) had no effect. Grass biomass peaked in 3 yr, then declined to negligible levels. Detrimental effects of both burning and seeding on native species appeared small and short-lived over a 5-yr period. Native plant species richness decreased after burning, but after 5 yr nearly equaled that of unburned areas. Native plant species richness was unaffected by seeding rate. Native plant cover increased with time after clearcutting regardless of treatment. In burned areas, seeding reduced native cover slightly. Exotic species richness and cover were highest in burned areas. About 25% of the planted western hemlock seedlings died, mostly during the first year. Mortality was 64% higher in seeded, burned areas than in unseeded, burned areas. Final seedling height was 4% higher in the burned than unburned areas, and seeding rate had no effect on height. Results of this study likely would apply to similarly treated western hemlock plant associations in coastal forests.

Introduction

Seeding forage grasses and legumes in recently burned clearcuts has been widely used in the western United States and Canada since the 1950s to increase the quantity of herbaceous forage for elk (*Cervus elaphus*), reduce ungulate browsing damage on conifer seedlings, suppress vegetation competing with conifer seedlings, or provide for erosion control (Ramsey and Krueger 1986, Owston et al. 1992, Powell et al. 1994, Becker et al. 1996). Seeding non-native grasses and herbs is also a widespread practice for erosion control and restoration of soil-nutrient cycles after wildfires (Klock et al. 1975, Tiedemann and Klock 1976, Agee 1993). Nevertheless, seeding programs are controversial (Owston et al. 1992).

Grasses compete with conifer seedlings, slowing growth or increasing mortality (Clark and McLean 1978, Crouch 1979, Dimock et al. 1983, Stewart et al. 1984, McDonald 1986, Bell et al. 2000), especially in moisture-limited sites (Clark and McLean 1978, Crouch 1979, Dimock et al. 1983). Seeding may increase herbivory by attracting ungulates (Crouch 1969, Hines and Land 1974, Becker 1989), rather than decrease herbivory by providing a high-quality forage alternative to conifer seedlings (Campbell and Evans 1975). Herbivory on woody plants from microtine rodents that flourish in dense grass swards created by seeding and fertilization also can be a problem (Lawrence et al. 1961, Askham 1992). Seeding typically introduces exotic or weedy species and potentially alters successional development of native plant communities (Tiedemann and Klock 1976, Helvey and Fowler 1979, Owston et al. 1992, Agee 1993, and see Becker et al. 1996 for review).

Changes in post-harvest management practices in western U.S. forests also have led to questions about the impact and value of forage seeding in logged areas. Air quality standards have forced a shift from fall burning of logging debris for site preparation and fuel reduction (Owston et al. 1992) to no burning or burning during the spring, when fire intensity and fuel reduction are relatively light (Miller et al. 1993). Cool spring burns leave more woody debris and impact native plant communities less than hotter fall burns (Dyrness 1973, Halpern 1988, Halpern and Spies 1995). Consequently, seeded grass production may be low because of limited availability of germination sites and from increased competition with residual

[1]Author to whom correspondence should be addressed. E-mail: jlehmkuhl@fs.fed.us

vegetation (Owston et al. 1992). Greater rates of seeding, however, might compensate for less germination space. Diminished, yet still potentially useful, amounts of forage in lightly burned areas might compete less with native species or planted conifers, especially in coastal areas with high rainfall. Not burning may reduce invasion of ruderal species (Isaac and Hopkins 1937, West and Chilcote 1968, Halpern et al. 1997) that are increasingly becoming an important issue for coastal forest management (DeFerarri and Naiman 1994, Heckman 1999, Thysell and Carey 2000).

Information to assess the interactive effects of new burning practices and forage seeding is limited. Grass seeding programs have been poorly monitored, many have had no experimental replication or control, predictability of effects is low because of high environmental variability among sites, and many studies have not been published in the scientific literature (Agee 1993, Powell et al. 1994, Becker et al. 1996). The goal of this study was to quantify experimentally the short-term (5 yr) effects of spring burning and rate of grass seeding on production of seeded forage, native and exotic plant species groups, and the survival and growth of planted conifer seedlings in a coastal western hemlock (*Tsuga heterophylla*) forest in western Washington. Because there were two replicates in the study and many species were sparsely distributed, I analyzed treatment effects on native and exotic plant species as groups, not individual species. An appendix of species responses is available from the author. I applied fertilizer with seed on seeded areas (the same amount regardless of seeding rate), but not to unseeded areas, to mimic typical forest management practices (Owston et al 1992; Mark Ostwald, Olympic National Forest, Quinault Washington, personal communication,). Hence, the seeding treatment was designed to compare the effects of no seed + no fertilizer vs. two rates of seed application + a constant amount of fertilizer. I did not explicitly test the effects of burning and seeding treatments on ungulate herbivory because that would have required a more geographically extensive experimental design than was feasible (Becker et al. 1996). However, I did measure and report the occurrence of small and large mammal herbivory on conifer seedling mortality.

I tested two hypotheses: 1) Spring burning, compared to no burning, will: (a) enhance the production of seeded forage; (b) reduce the short-term species richness and cover of native plants; (c) increase the species richness and cover of exotic species; and (d) enhance the survival and growth of planted conifer seedlings; 2) Increasing forage grass seeding rate will: (a) increase forage production; (b) decrease richness and cover of native plants; (c) increase the richness and cover of exotic species; and (d) decrease survival and growth of planted conifer seedlings.

Methods

Study Area

The experiment was in two clearcuts (15.0 ha and 9.3 ha) of the Bull timber sale, Olympic National Forest, located in the lower Matheny Creek drainage on the western Olympic Peninsula (latitude 47° 33'N; longitude 123° 57'W). The units were separated by a forested buffer of about 200 m. Forests at both sites were clearcut in January 1990 and yarded in March and April 1990. Experimental units were broadcast burned with a helitorch under clear weather during late May 1991, seeded with forage grasses in fall 1991, then planted with conifer seedlings during mid-February 1992. Seedlings were planted at a 3.3-m spacing, with 15 cm scalping of unburned sites only. Planting stock was a typical mixture of western hemlock plug 1-0 (50%), western redcedar (*Thuja plicata*) plug 1-0 (25%), and Douglas-fir (*Pseudotsuga menziesii*) bare-root 2-0 (25%) seedlings. Only western hemlock seedlings were sufficiently abundant in all plots (mean 31 seedlings, range 15-57) for measurement of treatment effects on seedling growth and survival. No seedlings were replanted. Data were collected during the fall from 1992 through 1996.

Forest vegetation in the study area is in the western hemlock series, with adjacent upslope areas in the Pacific silver fir (*Abies amabilis*) series. The dominant plant association is western hemlock/Alaska huckleberry-salal (*Tsuga heterophylla/Vaccinium alaskaense-Gaultheria shallon)* (Henderson et al. 1989). The topography is gently sloping (<10°) with a northerly aspect. Soils are highly productive, medium and moderately coarse-textured, moderately-deep till soils in the Mudcreek-Kalaloch complex typical of level remnant outwash terraces (Olympic National Forest 2000). Elevation at the site is about 200 m. Mean annual precipitation at a nearby weather station during the study period (1990-1996) was 292 cm

(range 224-343 cm), and mean annual temperature was 10°C (range 9-11°C) (NOAA 1997). Mean annual precipitation at the site likely was somewhat higher, approximately 330 cm (Henderson et al. 1989).

Experimental Design

I allocated burning and seeding treatments in a randomized complete block split-plot design, where each of the two clearcut units was a block (Federer 1955) (Figure 1). Burning was the whole-plot treatment. I randomly selected half of each block for spring burning and the other half was to be left unburned. However, because of the vagaries of burning clearcuts, about two-thirds of each block was burned. Burning occurred during April 1991.

Within burned and unburned whole-plots, I randomly assigned three seeding rates (0 kg/ha, 22 kg/ha, and 44 kg/ha) to split-plots of approximately 40 x 40 m (Figure 1). Only one split-plot of each seeding treatment was physically possible in the unburned area, but two split-plots of each seeding treatment were randomly located in the

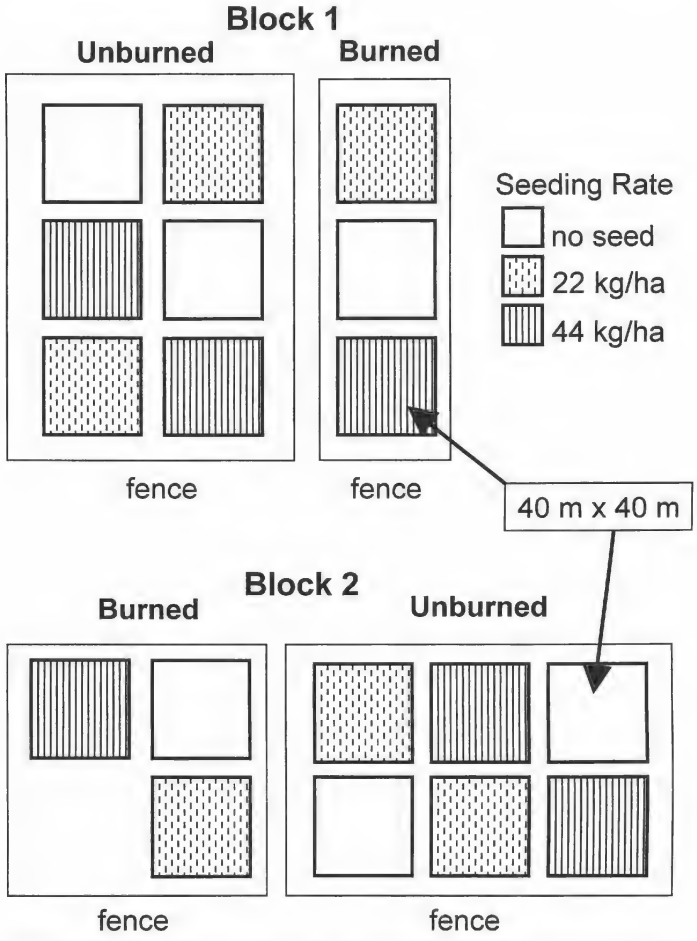

Figure 1. Experimental layout of whole-plot burn and split-plot seeding treatments to test the effects of spring burning and seeding rate on seeded grass production, native plant communities, and planted seedling mortality in the Matheny Creek drainage on the western Olympic Peninsula, Washington.

larger burned portion of each block. The unconventional use of two split-plots of each seeding treatment in burned areas was done to sample proportionately similar areas of the burned and unburned treatment areas. Thus, nine treatment split-plots were established in each of the two blocks. Details of the analysis of variance (ANOVA) model are in the Statistical Analysis section.

I applied seed and fertilizer during October 1991 with hand seeders to ensure accurate and homogeneous application. Following standard District management practices, I applied 16N-16P-16K elemental fertilizer only to seeded treatment plots at the rate of 336 kg/ha. The seed mix was 27% Potomac orchard grass (*Dactylis glomerata*), 21% white clover (*Trifolium repens*), 21% tetraploid perennial ryegrass (*Lolium perenne*), 21% birdsfoot trefoil (*Lotus corniculatus*), and 10% annual ryegrass (*Lolium multiflorum*) by weight. Germination rate certified by the seed company was 85% for orchard grass, 90% for annual ryegrass, 85% for perennial ryegrass, 82% for white clover, and 59% for birdsfoot trefoil. Legume seed was pre-inoculated with Dormal-brand nitrogen-fixing bacteria. The legumes, however, failed to germinate or became established at only trace levels. Seed and fertilizer also were applied selectively to areas outside and adjacent (within 50 m) to the experimental plots to lure deer and elk away from the experimental area.

The treatment area was enclosed with four strands of smooth wire electrified with a solar-powered charger to exclude black-tailed deer (*Odocoileus hemionus*) and elk. The fence functioned for about 1 yr, then the chargers failed and were not replaced. The fence remained standing, but did not totally exclude elk or deer. To estimate the potential effects of unplanned ungulate herbivory on dependent variables, I monitored elk and deer use by pellet-counts and incidence of browsing on planted conifer seedlings.

Field Measurements

National Forest personnel estimated pre- and post-burn amounts of woody debris in each block by the planar intersect method (Brown 1974), as implemented in standard Forest Service fuel inventories. Eight (Block 2) and 12 (Block 1) random debris plots were measured in blocks before burning, then remeasured after burning to estimate mean debris reduction for the entire burned portion of each block.

I measured the treatment responses of biomass production for seeded grasses, species richness and cover of native and exotic species, and growth and mortality of planted conifer seedlings in the central 20 x 20 m area within each treatment split-plot. Native and exotic species designations were based on Hitchcock and Cronquist (1973). Plant species cover <1 m tall was estimated from forty 20 x 50 cm quadrats (Daubenmire 1959, 1968) in each treatment split-plot. I located quadrats in each treatment split-plot along four permanent 20-m transects systematically located 4 m apart.

I placed the first quadrat 1 m from the end of the tape, and each successive quadrat at 2-m intervals along the transect. Cover was measured each year at the same points on the left side of the transects. I estimated aerial cover by cover classes (Daubenmire 1959), which minimized annual variation in cover estimates among different field personnel. Mid-points of cover classes were used in the analysis. I recorded elk or deer pellets in cover quadrats to estimate use of the treatment areas. I used line-intercept estimates along the permanent 20-m transects to estimate cover of vegetation ≥1 m tall.

I estimated the annual above-ground production of seeded forage biomass during the last 2 wk of September by clipping seeded grass and legume biomass at ground level within sixteen 20 x 50 cm quadrats per seeded treatment split-plot. I clipped four quadrats along each of the permanent sample transect lines at 4-m intervals on the opposite (right) side from the cover quadrats and 1 m away from the transect. Each year the position of the first clip quadrat was shifted 1 m up the transect to avoid previously clipped areas. Live material and standing dead material from the current year's growth was clipped. Clipped biomass was bagged and dried at 100°C (Milner and Hughes 1968) for 48 hr to determine dry weight.

I tagged all western hemlock seedlings planted within treatment split-plots during 1992 and monitored their survival annually for three growing seasons through 1995. I randomly selected 20 western hemlock seedlings in each treatment split-plot at the beginning of the study to measure height (measured at the end of the leader). At the end of

the 5-yr sample period, each split-plot had an average 18 western hemlock seedlings (range 8-23 seedlings/split-plot) to estimate average height for the treatment. Vegetation within a 2-m radius of tagged trees was not disturbed by biomass clipping and other measurements. I used the field guide by Lawrence et al. (1961) to identify which animal species browsed western hemlock seedlings.

Statistical Analysis

For each treatment split-plot, I calculated mean values of grouped native and exotic plant species cover, forage biomass, and conifer seedling survival and height from the individual quadrat or seedling measurements. Data for the two split-plot replicates of each seeding treatment within burned portions of blocks were averaged, which resulted in equal replication of seeding treatments per block (three burned and three unburned seeding values) for conventional blocked split-plot ANOVA designs (Federer 1955). The alternative to averaging for a balanced design was to exclude data for ~35% of the experimental area, which was deemed less desirable than averaging (Tim Max, US Forest Service, PNW Research Station, Portland, Oregon, personal communication).

I graphically determined how well data for dependent variables met the assumptions for ANOVA by examining for homogeneity of variance among groups and normality of distribution. A square root transformation ($\sqrt{(x + 0.5)}$) was applied to exotic species cover values, mortality and height data for western hemlock, and ungulate pellet frequencies to correct for uneven variance or skewed distributions.

I analyzed treatment effects on seeded grass production, native and exotic plant species cover and richness, seedling mortality, and ungulate use over the 5-yr study period by repeated measures ANOVA for a blocked split-plot design (Table 1). Seedling height and browsing occurrence were measured at the end of the experimental period, so I analyzed treatment effects on those variables without the repeated measures component in the ANOVA model. I did orthogonal contrasts to test elements of my hypotheses among levels of seeding, years, or cell means of the burning*seeding, year*burning, or year*seeding interaction terms if the main ANOVA indicated significant effects. SYSTAT (SPSS 1997) software was used for parametric statistical analysis.

TABLE 1. Analysis of variance model for a repeated-measures, randomized complete block, split-plot experiment to evaluate the effects of spring burning and forage seeding rates.

Source of Variation	df
Whole-plots	
Replicate	1
Burn	1
Error(a)	1
Split-plots	
Seeding	2
Seeding * burning	2
Error (b)	4
Repeated measures (5 yr)	
Time	4
Burn * time	4
Seed * time	8
Burn * seed * time	8
Error (c)	24
Total	59

A significance level of $P = 0.10$ was accepted for all statistical analyses. Although less conservative than $P = 0.05$, particularly with the relatively small sample size in this experiment (two replicate blocks), I considered $P = 0.10$ to be an acceptable chance of error for forest management issues and well within the bounds of statistical convention (Zar 1999). A significant difference is implied where a difference among means is reported in the text. For results presented primarily in figures, exact P-values are provided in the text to allow readers to assess the probability of error relative to their own standard of significance (Zar 1999).

Treatment effects on native and exotic plant assemblages were examined by canonical correspondence analysis (CCA) with the CANOCO program (Jongman et al. 1987, ter Braak 1988). Dependent variables were the mid-point of cover-class values for individual species in each of the 18 split-plots. Nominal independent environmental variables were the burning and seeding treatments for each split-plot. Block identification was entered as a covariate to control among-block variation for analysis of field experiments with CCA (ter Braak 1988). Rare species were downweighted.

The strength of the CCA ordination was represented by the trace, eigenvalues of the axes, and intraset correlations (Jongman et al. 1987). The eigenvalue is a measure of separation of the species distributions along the ordination axis, or the

amount of variation explained by the axis and environmental variables. The trace is the sum of all eigenvalues in the ordination. Intraset correlations measured the strength of association between the individual environmental variables and the ordination axes.

I tested the significance of the trace and the eigenvalue of the first axis by Monte Carlo permutation tests of 99 runs within the CANOCO program (ter Braak 1988). An observed trace and first eigenvalue significantly higher than calculated by the Monte Carlo permutations indicated significant multi-species differences in vegetation among the treatments.

I used biplots of species ordination scores and the centroids of the nominal environmental variable (treatment) scores (Jongman et al. 1987, ter Braak 1988) to display and interpret relationships of species groups to treatments. Treatment centroids represent the weighted average of treatment split-plot scores based on species composition. The locations of the species points and the treatment centroids jointly reflect the relative abundance of species, or collectively species groups, in relation to environmental gradients, in this case the treatments. Moreover, a location close to the origin indicates a relatively weaker relationship to the environmental gradient than a more distant location.

Results

Debris Reduction from Burning

Spring burning reduced total woody fuel by 19%, leaving from 92 to 142 Mg/ha debris in the two experimental blocks (Table 2). Fine (≤7.6 cm diameter) and large woody debris decreased 34% and 15%. Fuel depth overall was reduced 57%, to an average post-burn depth of 11 cm. An average 11 cm of duff remained after burning, which was an 18% to 29% reduction from initial conditions. Fuel moisture and fire behavior information were not collected by District fire staff who conducted the burn, which they characterized as a low-intensity, very good, early-spring prescribed burn (McCray 1991).

Ungulate Use

Elk and deer use of treatment plots was low (annual range 0.6 to 0.9 pellet groups/split-plot) and did not vary over the study period. Averaged across the study period, ungulate use was unaffected by burning, seeding, or their interaction. However, ungulates did use burned areas differently among years ($P = 0.10$) in apparent response to forage availability.

During the first year (1993) ungulates used unburned plots more heavily (1.25 pellet groups/plot) than burned plots (0.21 pellet groups/plot). Coincident with peak forage grass production in burned areas during the second and third years, ungulates switched to using burned areas (1994, 1.46 pellet groups/plot; 1995, 1.21 pellet groups/plot) while avoiding unburned areas (no pellets recorded). During the fourth year (1996), when grass production dropped markedly, use shifted away from burned areas (0.21 pellet groups/plot) back to unburned areas (1.67 pellet groups/plot).

Forage Production

Burning more than doubled the annual production of seeded grass ($P = 0.049$) (Figure 2). Peak production in 1994 averaged 977 kg/ha in burned areas, and 289 kg/ha in unburned areas. Grass production in both burned and unburned treatments was similar during the first 2 yr, increased

TABLE 2. Pre- and post-burn fuel characteristics in two experimental blocks for spring burning and grass seeding studies in the Bull timber sale, Matheny Creek, Washington during 1991. An asterisk indicates a significant change ($P \leq 0.10$) between mean pre- and post-burn amounts based on paired t-tests.

	Mean				Block 1 (n = 12)				Block 2 (n = 8)			
Fuel Type	Un-burned	Pre-burn	Post-burn	Change	Un-burned	Pre-burn	Post-burn	Change	Un-burned	Pre-burn	Post-burn	Change
Fine fuel (Mg/ha ≤7.6 cm)	32.4	32.0	21.1	-34%*	36.9	31.1	20.6	-34%	28.0	33.0	21.5	-35%
Large fuel (Mg/ha >7.6 cm)	127.6	112.1	96.3	-15%*	71.3	87.4	71.7	-18%	183.9	136.8	120.9	-12%
Total fuel (Mg/ha)	160.0	144.1	117.4	-19%*	108.2	118.5	92.4	-22%	211.8	169.7	142.4	-16%
Duff depth (cm)	11.4	15.4	11.4	-24%	13.0	21.1	15.0	-29%	9.9	9.7	7.9	-18%
Fuel depth (cm)	29.0	25.7	11.2	-57%*	31.5	25.1	8.4	-67%	26.4	26.2	14.0	-47%

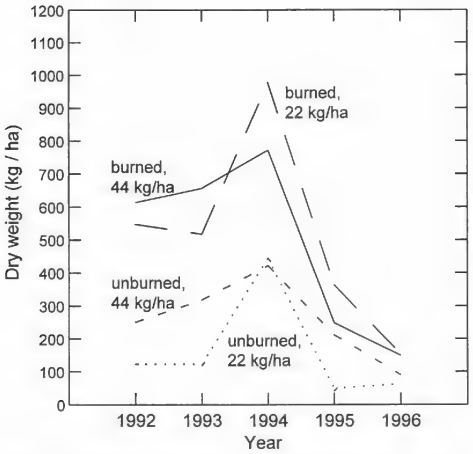

Figure 2. Mean dry weight production (kg/ha) of seeded orchardgrass and ryegrass from 1992 through 1996 in clearcuts with spring burning and seeding treatments.

markedly during the third year ($P = 0.001$), then declined during the subsequent 2 seasons to negligible amounts ($P < 0.001$). Doubling the rate of seeding from 22 kg/ha to 44 kg/ha had no overall effect on average annual production for the 4-year period, and annual differences between the two seeding rates were not different.

Plant Communities

Native Species

Richness of native species increased in all plots over time ($P < 0.001$), but, increased more rapidly in burned than in unburned plots ($P < 0.001$) (Figure 3a, b). Burned areas initially had fewer native species than unburned areas ($P = 0.006$), but richness more than doubled in burned areas during the subsequent 5 yr, while increasing only about 50% in unburned areas. At the end of 5 yr, burned areas averaged about three more native species than unburned areas ($P = 0.002$). Native species richness was unaffected by seeding treatments or by any interaction between seeding and burning.

Cover of native plants likewise increased with time after clearcutting ($P < 0.001$) (Figure 3c, d), with both burned and unburned areas recovering at similar rates. After 5 yr, however, burned sites had 10% less native species cover than unburned sites ($P = 0.001$). Seeding treatments affected native species cover differently in burned and unburned areas ($P = 0.063$). In burned areas, seeding (both levels combined) and fertilizing reduced native cover slightly (~3.5% over 5 yr) ($P = 0.005$) compared to unseeded burned areas. In contrast, seeding and fertilizing unburned areas resulted in 12% higher native cover than in unseeded unburned areas ($P < 0.001$). Positive responses of residual plants, primarily deer fern (*Blechnum spicant)* and residual or planted western hemlock seedlings, to seeding and fertilizing unburned areas appeared primarily responsible for the 12% treatment effect. However, another likely reason was that initial (1992) native plant richness and cover in those same unburned and seeded areas was nearly twice that of unburned unseeded areas ($P = 0.001$).

Exotic Species

More exotic species (about two species) were found in burned than unburned areas ($P = 0.018$) (Figure 4a, b). Trends in exotic species richness also differed between burned and unburned areas ($P = 0.054$). In burned areas, the number of exotic species increased during the first 3 yr, whereas, in unburned areas the number of exotic species remained relatively constant. Seeding had no effect on the number of exotic species, even though seed of five species of exotic grasses and legumes was introduced to seeded plots. There was no interactive effect of seeding and burning.

Burning increased exotic species cover by 3.5 times compared to unburned areas ($P = 0.094$). Cover of exotic species was higher in seeded than unseeded areas ($P=0.038$) (Figure 4c, d), even though the number of exotic species was unaffected by the seeding treatment. Exotic species cover decreased in seeded areas after 1994 ($P = 0.023$) as seeded grass cover dropped to low levels, while exotic species cover in unseeded areas increased slightly during that period ($P<0.001$). There was no interactive effect of burning and seeding on exotic species cover.

Multi-Species Compositional Analysis

Species assemblages differed among treatment plots as a result of burning and seeding (intraset r >0.84 with the first two ordination axes) (Table 3, Figure 5). Burning had the strongest influence on species composition (Axis 1, 60-66% of trace

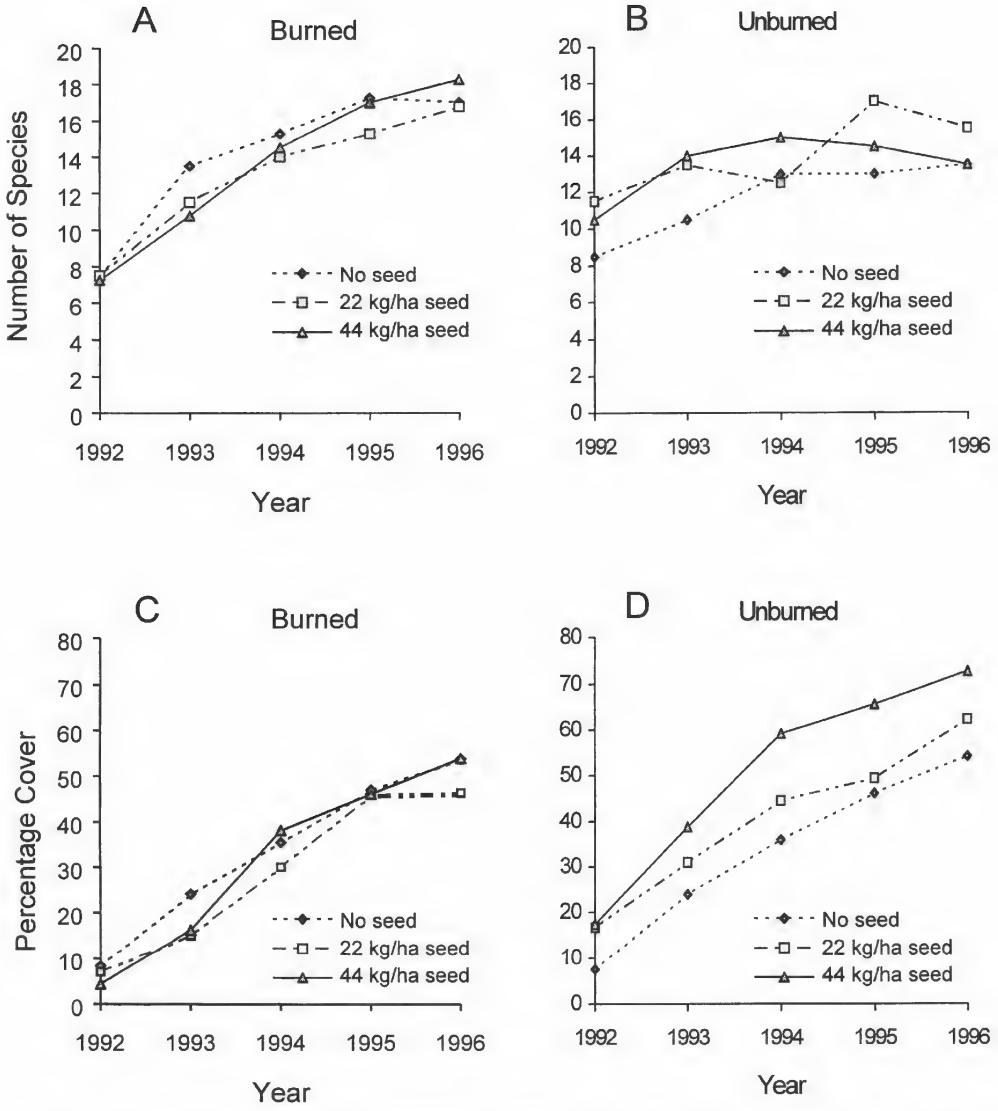

Figure 3. Species richness and canopy cover of native plant species from 1992 through 1996 in clearcuts with spring burning and seeding treatments.

variation across years). Seeding treatment had a weaker effect on species composition (Axis 2, 24-30% of trace variation across years).

Treatment effects weakened and species assemblages became more similar over time. Differences among plots were strongest in 1992 immediately after treatment, when treatments accounted for 64% of the variation (i.e., the trace of ordination) in species composition among plots (Table 3). Plots became more similar over the subsequent 4 yr, as indicated by progressively smaller ordination traces and eigenvalues, and a shift of treatment centroids (group means) toward the origin of the ordination space (Figure 5). By

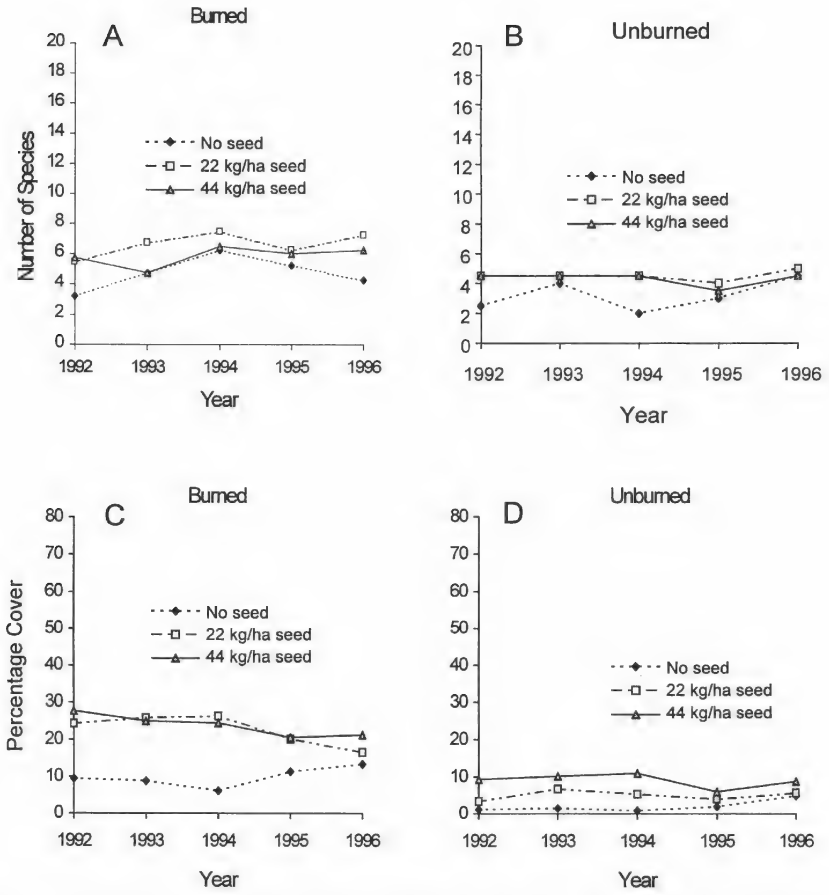

Figure 4. Species richness and canopy cover of exotic plant species from 1992 through 1996 in clearcuts with spring burning and seeding treatments.

TABLE 3. Canonical correlation analysis of the effects of spring burning and grass seeding rates on plant assemblages in clearcuts. All trace values and first eigenvalues (second eigenvalues were not tested) were significant ($P \leq 0.10$) as determined by Monte Carlo permutation tests.

	1992 Axes		1994 Axes		1996 Axes	
	1	2	1	2	1	2
Trace[a]	0.638		0.378		0.212	
Eigenvalue	0.405	0.191	0.250	0.093	0.128	0.062
Percentage variance[b]	63.4	29.9	66.2	24.7	60.6	29.1
Intraset correlation[c]						
Burned	-0.940	0.333	-0.845	0.537	-0.954	0.403
Unburned	0.940	-0.333	0.845	-0.537	0.954	-0.403
No seed	0.265	0.857	0.555	0.845	0.308	0.852
22 kg/ha seed	-0.002	0.069	-0.238	-0.192	0.090	0.124
44 kg/ha seed	-0.202	-0.728	-0.230	-0.515	0.369	0.901

[a] Sum of four eigenvalues. Proportion of variation in species data accounted for by ordination.

[b] Percentage of total explained variance (trace) accounted for by ordination axes.

[c] Correlation coefficients of environmental variables with ordination axes.

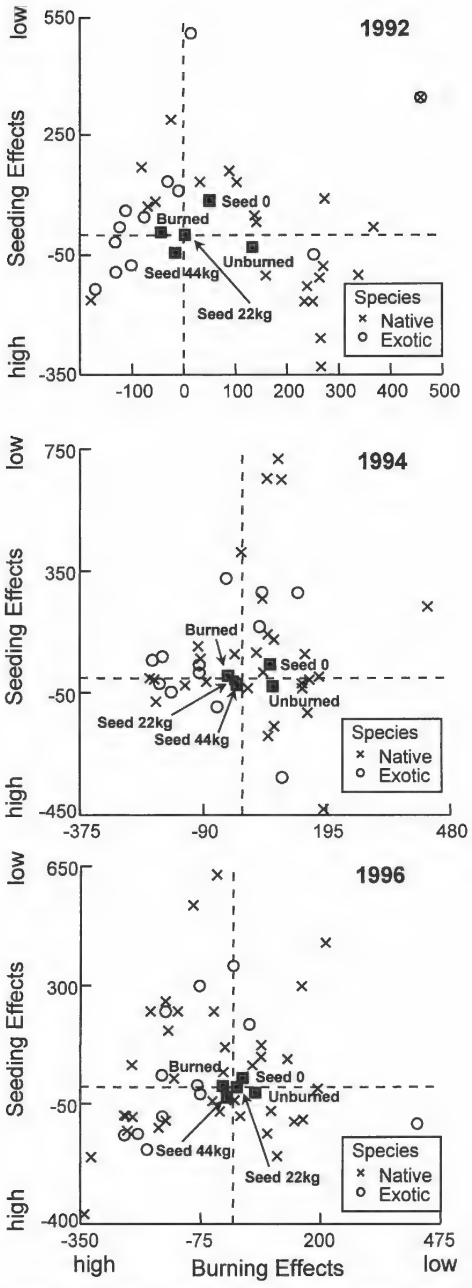

Figure 5. Biplots of plant species ordination scores and the centroids of treatment scores estimated by canonical correspondence analysis in clearcuts with spring burning and seeding treatments during 1992, 1994, and 1996.

the fifth year, only 21% of the variation (trace) in species composition among plots was associated with treatments. Exotic species continued to be most abundant in burned areas, whereas the distribution and abundance of native species became poorly associated with burning history, as indicated by a broad distribution of species along the primary burning gradient (Axis 1) (Figure 5).

Seedling Survival and Growth

An average of 25% of the planted western hemlock seedlings died over three growing seasons (1993-95) (Table 4). Nearly all (87-100%) mortality occurred during the first two growing seasons after planting. Burning and seeding treatments alone had no effects on seedling mortality, but their interaction affected seedling mortality in contrasting ways ($P = 0.053$).

TABLE 4. Mean cumulative proportion of dead western hemlock seedlings planted in clearcuts with spring burning and seeding treatments. Analysis of variance tested results for 1995 only. Means with similar superscripts were not significantly different ($P > 0.10$). The interaction between burning and seeding treatments was significant.

		Seeding Rate			
Treatment	Year	No seed	22 kg/ha	44 kg/ha	Mean
Burned	(n=131)	(n=142)	(n=110)	(n=383)	
	1993	0.184	0.286	0.289	
	1994	0.202	0.332	0.328	
	1995	0.202	0.332	0.328	0.287[a]
Unburned		(n=57)	(n=39)	(n=75)	(n=171)
	1993	0.328	0.202	0.123	
	1994	0.328	0.202	0.123	
	1995	0.328	0.202	0.123	0.218[a]
Mean	(1995)	0.265[a]	0.267[a]	0.225[a]	0.252

Seedling mortality in burned areas was 64% higher in seeded and fertilized plots than in unseeded plots ($P<0.01$) (Table 4). In contrast, seeding (combined effect of both rates) and fertilizing unburned areas decreased mortality by 31% compared to unseeded unburned areas ($P<0.001$).

Damage by wildlife, both ungulates and small mammals, appeared to be a minor factor in western hemlock seedling mortality. Only 3.8% of the 554 tagged seedlings were browsed, and only 1.4% of all western hemlock seedlings were both

browsed and dead at the end of the study. After 5 yr, cumulative browsing incidence was higher in unburned areas (5.4%) than in burned areas (3.4%) ($P = 0.011$). Seeding and fertilization had no effect on incidence of browsing, and there was no interactive effect of burning and seeding on browsing.

Treatment effects on western redcedar seedling mortality were not tested because of an incomplete distribution of seedlings among treatment plots. However, simple inspection of the data regardless of treatments showed that western redcedar seedlings had slightly less mortality than did western hemlock, with about 21% mortality among the 327 tagged western redcedar seedlings. Western redcedar seedlings were more heavily browsed than western hemlock, with 74.3% incurring some browsing, primarily by mountain beaver (*Aplodontia rufa*) or snowshoe hare (*Lepus americana*). About 12% of all tagged western redcedar seedlings were both browsed and dead vs. 1.4% for tagged western hemlock.

Initial heights of planted western hemlock seedlings were not different in treatment plots, but after 3 yr seedlings were about 4% taller in burned than in unburned areas ($P = 0.062$) (Table 5). Seeding treatments had no effect on final seedling height, nor was there an interactive effect of burning and seeding rate.

TABLE 5. Mean height (cm) of planted western hemlock seedlings after 3 growing seasons (1992–1995) in clearcuts with spring burning and seeding treatments. Means with different superscripts were significantly different ($P \leq 0.10$). The interaction between burning and seeding treatments was not significant.

	Seeding rate			
Burn treatment	No seed	22 kg/ha	44 kg/ha	Mean
Burned	277	269	286	277[a]
Unburned	273	283	250	267[b]
Mean	276[a]	273[a]	273[a]	274

Discussion

Forage Production

As hypothesized, burning enhanced the production of seeded forage grasses (Figure 2). Higher production in burned areas likely was a function of better germination conditions from reduction of duff and woody debris to ash (Klock et al. 1975, Tiedemann and Klock 1976, Agee 1993), an immediate flush of available nutrients in burned sites from reduction of organic matter (Grier et al. 1989, Agee 1993), and less competition from native plants (Stewart et al. 1984, McDonald 1986, Owston et al. 1992) than in unburned sites. Unburned sites had initial post-treatment (1992) plant cover nearly double that of burned areas, and subsequent growth of residual native plants was rapid; hence, competition with residual vegetation likely limited forage production in unburned vs. burned areas. Bell et al. (2000) found that herbaceous plant cover was a good indicator of competitive relations between herbaceous and woody species.

Doubling the rate of seeding did not affect production (Figure 2). Consequently, managers could not compensate for poor conditions for grass germination or growth in unburned areas by increasing the seeding rate. Grass production in burned areas, primarily orchardgrass, was low compared to other studies. Peak production of about 1,000 kg/ha biomass in spring burned areas was reached during the third year after a relatively heavy seeding of 22 kg /ha. In contrast, Powell et al. (1994) measured 1,251 kg/ha production of orchardgrass from only 0.5 kg seed per ha applied to clearcut and fall-burned sites in drier lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*) sites in interior British Columbia.

Plant Communities

The hypothesis that spring burning reduces the richness and cover of native plants over a 5-yr period was rejected (Figure 3). The primary driver of successional change in native plants was the removal of the canopy by clearcutting and the subsequent growth of residual native species (Dyrness 1973, Alaback 1982, Stein 1995, Halpern and Spies 1995), primarily deer fern, salal, salmonberry (*Rubus spectabilis*), and western hemlock seedlings. Immediately after burning, native plant species richness and total cover were lower in burned plots than unburned plots. Within 5 yr, however, recovery of native species richness and cover differed little between unseeded burned and unburned stands. Species richness was initially lower in burned sites than unburned sites in the Oregon Cascades and Coast Range, but differed little between treatments after 4-7 yr (Dyrness 1973, Halpern 1988, Schoonmaker and McKee 1988,

and Stein 1995). Likewise, shrub cover was immediately lower in burnt than in unburnt stands in the central Oregon Cascades, but did not differ after 7 yr (Steen 1966). However, shrub and herb species compositions varied after 7 yr, depending on the species dominating the site after treatment.

Burning increased the richness and cover of invading exotic species as predicted (Figure 4). Dyrness (1973) and Halpern (1988) found similar differences in exotic species cover between lightly burned and unburned sites. They observed that differences among treatments were a function of the interaction between treatment effects and species life history and phenology. Similarly, in this study exotic species cover declined in burned areas as seeded grass cover declined, whereas in similarly burned, but unseeded, areas increasing exotic herb cover drove overall increases in exotic species cover.

The presence of seeded forage grasses had little apparent long-term effect on native plant communities (Figure 4). Grass biomass declined to negligible levels after 5 yr. The only effect of the seeding treatment on native plants occurred in unburned areas, where native species cover counterintuitively was higher in seeded than in unseeded plots. Initially higher native species cover on unburned seeded vs. unseeded plots could explain much of that difference. Fertilization of unburned and seeded plots, as a component of the seeding treatment, also might explain the greater response of native species to seeding unburned plots. However, the response of common native species to fertilization varies by species and fertilizer composition (Prescott et al. 1993, Thomas et al. 1999, He and Barclay 2000). No conclusions about individual native species responses can be confidently made from this small sample.

Seedling Survival and Growth

Western hemlock seedlings grew taller (4%) in burned than unburned areas as predicted (Table 5). That result supports site preparation practices that eliminate competing vegetation to maximize western hemlock seedling survival and growth (Scott 1962, Ruth 1976). Seedling survival was affected by burning, but only if the site was seeded afterward (Table 4). On burned sites, seedling mortality was 64% higher with seeding than without seeding, most likely because of competition with seeded grasses. Western hemlock is a shallow rooted species (Packee 1990) with slow seedling growth rates (Ruth 1976), and orchard grass is a strong competitor with conifer seedlings (Tiedemann and Klock 1976, Clark and McLean 1978, Powell et al. 1994) even at <10% foliar cover (Tiedemann and Klock 1976). Cover of seeded grasses in burned and seeded plots was 15% and 23% during the first two growing seasons after planting when most mortality occurred. On unburned sites, however, the opposite was true. Mortality was higher on unseeded sites, where fertilizer had not been applied as part of the seeding treatment, than on seeded and fertilized sites, possibly as a result of greater competition for nutrients with native species (Stewart et al. 1984, McDonald 1986, McDonald and Radosevich 1992). These complex relationships point to the need for controlled manipulative experiments to test for competitive interspecific interactions between species among treatments (e.g. Powell et al. 1994, Halpern et al. 1997).

Herbivory

Both small mammals (snowshoe hare and mountain beaver) and ungulates browsed western hemlock seedlings during the first year after planting. Burning affected herbivory, but seeding did not appear to reduce (Campbell and Evans 1975) or facilitate (Crouch 1969, Hines and Land 1974, Becker 1989) herbivory. Relatively high cover of residual vegetation in unburned vs. burned plots facilitated seedling herbivory by providing cover for small herbivores (Lawrence et al. 1961, Owston et al. 1992). In burned areas, herbivory was low because residual cover was poor and because seeding did not produce grass swards dense enough for small mammal cover. Cover apparently was insufficient to facilitate a population eruption of voles (*Microtus* spp.), which can effectively control woody vegetation through herbivory (Lawrence et al. 1961, Haufler and West 1986, Askham 1992).

In conclusion, many of the hypothesized treatment effects were supported either as main effects or interactions. Spring burning of clearcuts had relatively greater impacts than seeding and fertilizing on plant communities. High forage seeding and fertilizer application rates and their associated costs, the short productive period, poor production in unburned areas, and competition with conifer seedlings in burned areas should be weighed against the relatively short-term benefits

of forage seeding. Results of this study likely would apply to similarly treated western hemlock plant associations in coastal forests. However, managers should apply these results with caution and the understanding that substantial variation may occur in species responses to management treatments depending on site conditions (Scott 1962), species life histories, and variation in disturbance effects (Halpern 1988, Halpern et al.1997). The complexity of the discovered treatment effects and the need to examine species competitive interactions more carefully both suggest the need for more extensively replicated and narrowly defined studies.

Acknowledgements

This project was part of the Matheny Cooperative Elk Study conducted by the USDA Forest Service, Pacific Northwest Research Station and Olympic National Forest, and the Washington Department of Fish and Wildlife. Additional funding was provided by the Rocky Mountain Elk Foundation. The Olympic National Park, Quinault Indian Nation, Washington Department of Natural Resources, University of Washington, Washington Bowhunters Association, and the Kitsap Bowhunters Association also contributed time or resources. Expert field assistance was provided by J. Vandermark, M. Ostwald, K. March, B. Lyons, K. Peterson, C. Hansen, K. Sloan, E. Kuhlmann, N. Setunsky, and C. McDonnell. Special thanks to M. Ostwald, R. Mayte, C. McDonnell, J. Lowrie, D. Warrington, and T. Beddow, Quinault District Ranger, for providing the technical, financial, and administrative support to perform the treatments and collect data. J. Agee, R. Miller, J. Henderson, and A. Tiedemann reviewed an early draft of the manuscript. C. Halpern and M. Newton provided insightful comments to second draft. T. Max advised on the experimental design and analysis of variance, and reviewed the manuscript. E. D. Ford also provided a statistical review of the manuscript.

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Received 11 December 2000
Accepted for publication 23 July 2001

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B. H. K. Wolter and **R. W. Fonda,** [1,2] Biology Department, Western Washington University, Bellingham, Washington 98225

Gradient Analysis of Vegetation on the North Wall of the Columbia River Gorge, Washington

Abstract

The Columbia River Gorge represents an ecocline of shifting environmental factors, species populations, and vegetation associations. Combinations of wind, temperature, and precipitation create different environmental regimes from the west to the east. The north wall of the Gorge supported four physiognomic associations: western conifer forest, central mixed forest, central broadleaf forest, and eastern steppe. Each association comprised species distributed individually along the ecocline. Douglas-fir, western redcedar, bigleaf maple, dull Oregongrape, sword fern, bracken, vine maple, and red bilberry were centered in the western conifer forest. Garry oak, ponderosa pine, poison oak, and snowberry were centered in the central mixed forest. Cheatgrass, northern buckwheat, Wyeth's lupine, western serviceberry, mockorange, and Sandberg's bluegrass were centered in the eastern steppe. Although the center of distribution for each species was in one of the associations, few were confined to a specific association. The Columbia River Gorge is analogous to a mountain turned on its side, with the cool, moist summit to the west and the warm, dry base to the east. Plant species have migrated both eastward and westward along this ecocline during the lifetime of the Gorge, and each association has combinations of species derived from surrounding regions in Washington and Oregon.

Introduction

The Cascade Mountains are a major geographical barrier between distinctly different vegetation formations in Washington and Oregon. The cool, moist forests that lie west of the Cascades in both states, influenced by the prevailing maritime climate, contrast with the warmer, drier shrub-grass steppe, influenced by the prevailing continental climate, to the east of the mountains. The Columbia River cuts through the Cascade Mountains between Washington and Oregon (Figure 1) forming a gorge that has served as a migratory corridor between these two vegetation formations for millennia (Lawrence 1939, Detling 1958, Franklin and Dyrness 1988). The modern vegetation in the Columbia River Gorge (CRG) is a product of species from surrounding regions overlapping according to the varied habitats available in the Gorge (Detling 1958). Species distribution throughout the length of the CRG is regulated by climate (Lawrence 1939). The western CRG is cooler and wetter than the eastern CRG (Lawrence 1939, Lynott 1966, National Oceanic and Atmospheric Administration 2000). Wind is an important environmental factor in the CRG. Mean annual wind velocity is 12.8 km/hr (National Oceanic and Atmospheric Administration 2000). Gusts exceeding 190 km/hr were measured at Crown Point, Oregon, 8 km southeast of Washougal (Lynott 1966). Prevailing winds are from the west, but during winter, with a high pressure system in place over the Columbia Basin, exceptionally strong winds can blow from the east (Lawrence 1939, Lynott 1966, Sinton et al. 2000). For example, two winter storms in 1973 and 1983 created extreme northeast winds that caused windthrow in 8% of the forest in the Bull Run watershed, near the western end of the CRG in Oregon (Sinton et al. 2000). Because the walls on the north and south sides of the CRG face opposite directions, local climate differs markedly between Washington and Oregon locations. Compared to the south wall of the CRG, the growing season environment of the north wall is characterized by greater solar radiation, higher air and soil temperatures, and greater evapotranspiration. These factors typically combine to cause low vegetation cover (Cleary and Waring 1969, Barbour et al. 1999). Wind desiccation, combined with greater solar radiation, makes the north wall of the CRG considerably warmer and drier than the nearby upland forests of the Willamette Valley and the montane forests of the Cascade Mountains. On the north wall, local wind, temperature, and moisture differ according to slope aspect associated with individual habitats. Local differences

[1]Author to whom correspondence should be addressed. email: fonda@biol.wwu.edu

[2]Edward G. Schreiner, past editor of Northwest Science, served as editor for this paper

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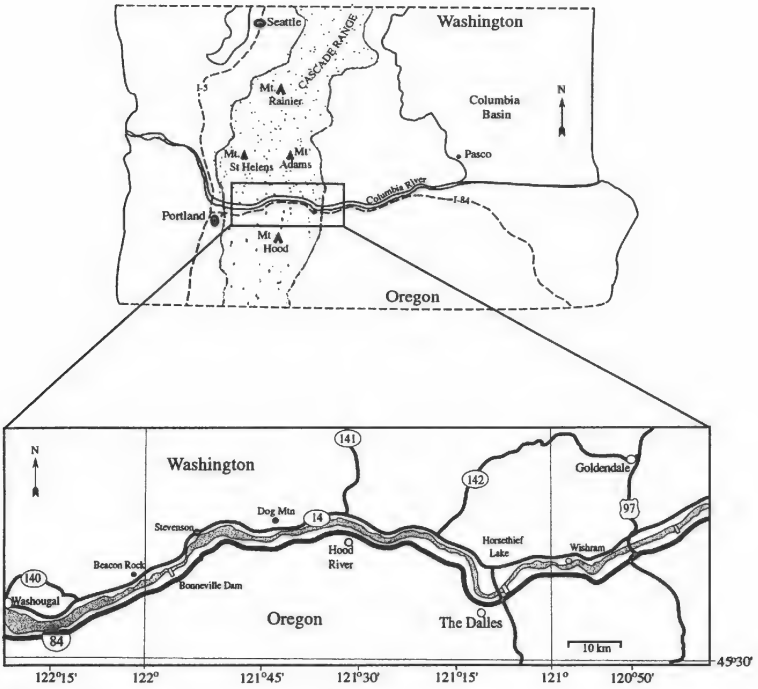

Figure 1. The study area, located on the Washington side of the Columbia River, extended from the western end of the Gorge at Washougal to the eastern end at Wishram.

among slope aspects and ravines clearly affect values of solar radiation, wind, temperature, and moisture (Barbour et al. 1999). During the growing season, southwest and south slopes are more exposed to higher wind, solar radiation, and temperature, making them drier than southeast slopes in the same location. Ravines are more protected from wind, are moister, and have lower ambient temperatures. Considering the entire ecocline in the CRG during the growing season, the eastern CRG is drier and hotter than the western CRG. On a microsite scale, southwest slopes are hotter and drier than southeast slopes. In sum, the CRG is an ecocline (Whittaker 1967) through which a mosaic of environmental factors and plant species vary in parallel.

The Columbia River is antecedent to both the Cascade and Coast Mountains of Washington and Oregon (Alt and Hyndman 1984). Three volcanic peaks are within 35 km of the CRG (Figure 1). Repeated basaltic floods during lower Miocene created the platform from which the Columbia Gorge was later carved (Baldwin 1966) from late Oligocene to middle Miocene as the high peaks of the Cascade and Coast Ranges rose and the river maintained its original flow (Alt and Hyndman 1984). The present soils in the CRG are formed in loess and fluvial deposits from the last advance of Pleistocene ice (Allen 1979). The CRG currently is a major thoroughfare through the Cascade Mountains, with railroads and state highways on both sides, and Interstate Highway 84 on the Oregon side (Figure 1). Within the CRG are state parks, the southern edge of the Gifford Pinchot National Forest (Washington), and some American Indian trust lands.

Two previous studies examined the distribution of plant species in the CRG. Lawrence (1939) provided a purely descriptive overview of the vegetation. He observed a wind gradient in the CRG, identified a general east-west environmental gradient, and noted that the vegetation of the north

TABLE 1. Mean maximum and minimum temperatures (°C) at four locations in the Columbia River Gorge, from west to east. Data are summarized from National Oceanic and Atmospheric Administration (2000).

	Mar-May		Jun-Aug		Sep-Nov		Dec-Feb	
	Max	Min	Max	Min	Max	Min	Max	Min
Washougal	19.2	2.0	25.7	9.1	22.6	2.9	8.3	-0.1
Bonneville Dam	19.1	3.2	25.9	11.3	23.2	4.4	8.4	0.3
Hood River	20.3	1.3	27.1	9.8	23.8	1.1	7.8	-2.5
The Dalles	22.9	2.0	30.7	12.4	26.7	1.8	8.9	-2.2

wall differed qualitatively from the corresponding south wall. Lawrence (1939) emphasized the severe winds and their impact on species distribution and plant morphology. Hydroelectric dams have since flooded many of the habitats Lawrence (1939) described. Later, Detling (1958) identified five distinct elements in the CRG flora, based on centers of distribution in surrounding regions. Of the 206 species described by Detling (1958), 34% were distributed widely in northwest North America, and another 26% were prominent in the Puget Trough area west of the Cascade Mountains. The Columbia Basin contributed 13% of the flora, and high elevations in the Cascades another 15%. Perhaps the most interesting element came from the Rogue River area in southwest Oregon, accounting for 8% of the flora. Seven species (3%) were endemic to the CRG. Detling (1958) did not analyze vegetation patterns and environmental relationships. The patterns created by vegetation associations and individual species on the north wall have not been studied.

Whittaker and Niering (1965) used gradient analysis to describe vegetation pattern in the Santa Catalina Mountains, Arizona. They showed that plant species were distributed individually, and that the vegetation pattern depended on environmental gradients created by elevation and slope aspect in the mountains. Gradient analysis has been used successfully to analyze and describe vegetation patterns of large and small areas (Whittaker 1960, 1961; Disraeli and Fonda 1979; Price et al. 1995; Lefstad and Fonda 1995; Sagers and Lyon 1997; Ohmann and Spies 1998).

We analyzed vegetation patterns on the north wall of the CRG by gradient analysis to describe the relationship between environmental factors and species distribution. Our objectives were to clarify how species are distributed in the CRG in relation to the regional climate through the CRG, and to microhabitats created by slope and ravine topography.

Methods

The study area was on the Washington (north) side of the 97 km Columbia River Gorge (Figure 1). The western end of the Gorge is located at Washougal, Washington (122° 15' longitude), and the eastern end is near Wishram, Washington (120° 50' longitude). Two cities, Hood River and The Dalles, Oregon, are located in the CRG, as are two hydroelectric dams at Bonneville and The Dalles (Figure 1). We limited our study area to sites ≤200 m above the Columbia River, because we wanted to ensure that the vegetation with which we worked was influenced only by the Gorge, not by the adjacent Cascade Mountains.

A general trend of increasing wind velocity (Lynott 1966), increasing summer temperatures (Table 1), decreasing winter temperatures (Table 1), and decreasing growing season precipitation (Table 2) defines the west-to-east environmental gradient in the CRG. Maximum temperatures are most consistent throughout the CRG during the December-May period, but they begin to diverge in June (Table 1). Differences of 4-5° between western and eastern stations last into September. Although minimum temperature differences exist among the stations, the range is less than among maximum temperatures. The lowest minima are in the east during September-February, but they are too variable to demonstrate a pattern during March-August (Table 1). Mean annual temperatures

TABLE 2. Mean average precipitation (cm) at four locations in the Columbia River Gorge, from west to east. Data are summarized from National Oceanic and Atmospheric Administration (2000).

Station	March–August	September–February	Annual total
Washougal	72.0	141.1	213.1
Bonneville Dam	57.1	138.8	195.9
Hood River	18.4	58.4	76.8
The Dalles	7.9	27.3	35.2

do not vary greatly between the western (10.5°C) and eastern ends (9.3°C) (National Oceanic and Atmospheric Administration 2000). The total amount of precipitation falling from March to August is an important component of the environmental gradient, because total growing season values are dramatically different between the ends of the CRG. March-August precipitation averages ~60-70 cm in the west but ~8-18 cm in the east (Table 2). Annual totals are similar between Washougal and Bonneville Dam, but The Dalles averages about half the total precipitation recorded at Hood River.

Data were gathered on species in the tree canopy, tall understory, and low understory layers using thirty-seven 20 x 50 m macroplots, at 18 locations at ~6' longitude intervals between Washougal and Wishram (Figure 1). Most locations were on public lands accessible along Washington State Route 14 (Figure 1). Obviously disturbed or managed locations, such as logged forests, abandoned fields, and grazed pastures, were avoided, although undoubtedly the entire study area no longer is pristine. Macroplots were situated on southwest (210-191°), south (190-170°), and southeast (169-150°) slope aspects, and in ravines at each sample location, when the location had such sites available. Macroplots on slopes were oriented with the central 50-m axis bearing 180°, and those in ravines were oriented with the long axis parallel to ravine bottoms. We located the macroplots using a random number table. For example, a macroplot on a south slope was located by first randomly choosing how far up the slope to proceed. Once that point was reached, a baseline was stretched parallel to the slope contour, then a random number was selected to represent the starting corner for the macroplot.

For trees >1 cm diameter at breast height, density was calculated as trees/ha for the entire macroplot. For tall and low understory species, cover was estimated to the nearest 1% for 1-10% cover, and nearest 5% for >10% cover, on twenty-five 20 x 50 cm microplots placed every 5 m along five 50-m lines in each macroplot. Cover and frequency were calculated from these data for each macroplot.

Prominence values were calculated for each species as PV=mean % cover * frequency$^{1/2}$ (Fonda and Bernardi 1976; Risvold and Fonda 2001). We entered density/ha for trees and PV for understory species into a detrended correspondence analysis (DCA) program in PC-ORD (McCune and Mefford 1995) to elucidate relationships among the 37 macroplots.

Botanical nomenclature follows Hitchcock and Cronquist (1973). Voucher specimens are deposited in the Biology Department herbarium (WWB) at Western Washington University.

Results

DCA Ordination

The two-dimensional DCA ordination we constructed used all 37 macroplots. The eight ravine macroplots were embedded in the overall ordination matrix, but for clarity in understanding relationships through the CRG and among the three slope aspects, the ravine plots were omitted from Figure 2. The ordination confirmed that the distributional pattern of the macroplots was continuous through the CRG (Figure 2). The X-axis reflects floristic changes from west to east, whereas the Y-axis reflects relatively moister conditions low on the axis to relatively drier conditions higher on the axis. The ordination also shows the relative positioning of macroplots according to slope aspect. Most of the forested macroplots on southeast slopes (#1, 6, 10, 13, 20, 23) were clustered to the left of the ordination, at values <200 (Figure 2). In contrast, many of the forested macroplots on southwest slopes (#15, 21, 28) were arranged toward the center (values of 285-374). Plots 18, 19, and 20 represent a good example of this ordination alignment. All three were located on Dog Mountain (Figure 1). Plot 18, on the southwest slope, aligned to the right, in contrast to #20, a southeast slope that aligned to the left. Plot 19, on the south slope, aligned between #18 and #20. Plot 18 was a stand of Garry oak (*Quercus garryana*) with much cheatgrass (*Bromus tectorum*) and poison oak (*Rhus diversiloba*) in the understory, whereas #20 was a stand of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) with an understory of snowberry (*Symphoricarpos albus*), dull Oregongrape (*Berberis nervosa*), and sword fern (*Polystichum munitum*). Plot 19 was a mixture of ponderosa pine, Douglas-fir, and Garry oak, with a complex understory of poison oak, dull Oregongrape, cheatgrass, and snowberry.

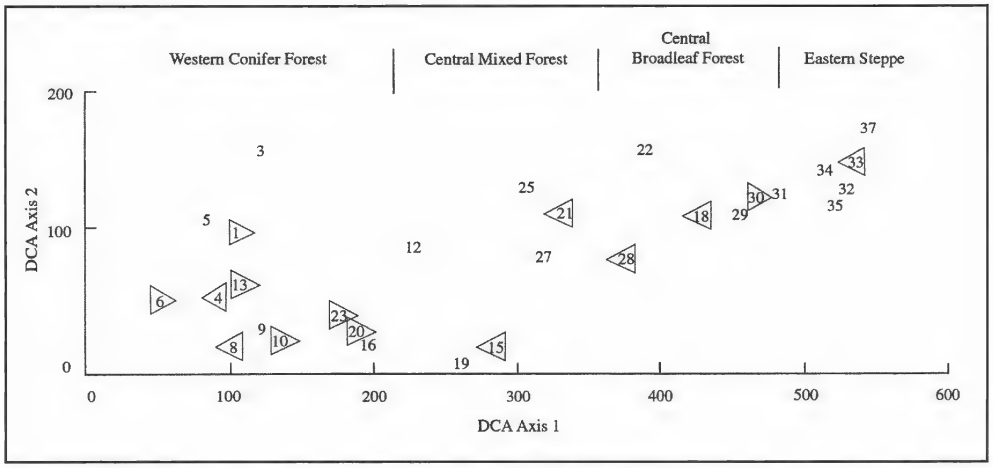

Figure 2. Two-dimensional DCA ordination of the 37 macroplots. Plot numbers inside ⌓ were on southwest slopes, those inside π were on southeast slopes, and those with no symbol were on south slopes. Plots in ravines were omitted from this figure.

Mosaic Diagram

After constructing the ordination, we inspected the data from each macroplot individually to identify patterns associated with tree density and mean cover of understory species. We combined these data and DCA patterns with forest physiognomy (either conifer dominance, mixed dominance, broadleaf dominance, or treeless) to create a mosaic diagram (Whittaker and Niering 1965) that identifies patterns associated with four physiognomic associations and the important plant species on the north wall (Figure 3). Plant species were distributed individually according to local and regional differences within the CRG, creating mixtures of dominant and subordinate species (Figure 3; Tables 3, 4). Within each association, ravines supported species combinations whose architecture differed from the surrounding slopes. In general, the total number of tree species and conifers declined eastward, whereas broadleaf trees increased eastward. In the understory, general indicators of moisture changed from west to east. For example, ferns were more prominent in the west, whereas graminoids were more prominent in the east. Of all the understory species, only cheatgrass averaged ≥50% cover on at least some locations in the study area. In each association, more than half the species present averaged <5% cover.

Western Conifer Forest Association

The western conifer forests extended from the western end of the CRG at 122° 15' to 121° 40' longitude (Figure 3). Coniferous trees in these forests were twice as dense as broadleaf trees. Macroplots in this association were dominated by Douglas-fir, which was uniformly dominant with high density and basal area over all slope aspects (Table 3), with 100% frequency. Eight other tree species were present in this association, of which bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) were the most prominent. Together these two subordinate species had about half the density of Douglas-fir, but much less basal area. Douglas-fir, bigleaf maple, and red alder were the only tree species on southwest slopes in the western conifer forests, whereas all tree species except Oregon ash (*Fraxinus latifolia*) and soft-leaved willow (*Salix sessilifolia*) grew on southeast slopes (Table 3). Western hemlock (*Tsuga heterophylla*) and grand fir (*Abies grandis*) were largely unimportant.

The understory of the western conifer forests was lush. No species accounted for >40% cover, frequency commonly was 30-60% for dominant species, and individual values for cover varied by slope aspect, yet the many species present in the forest contributed to the uniform structure of the understory. Sword fern, vine maple (*Acer*

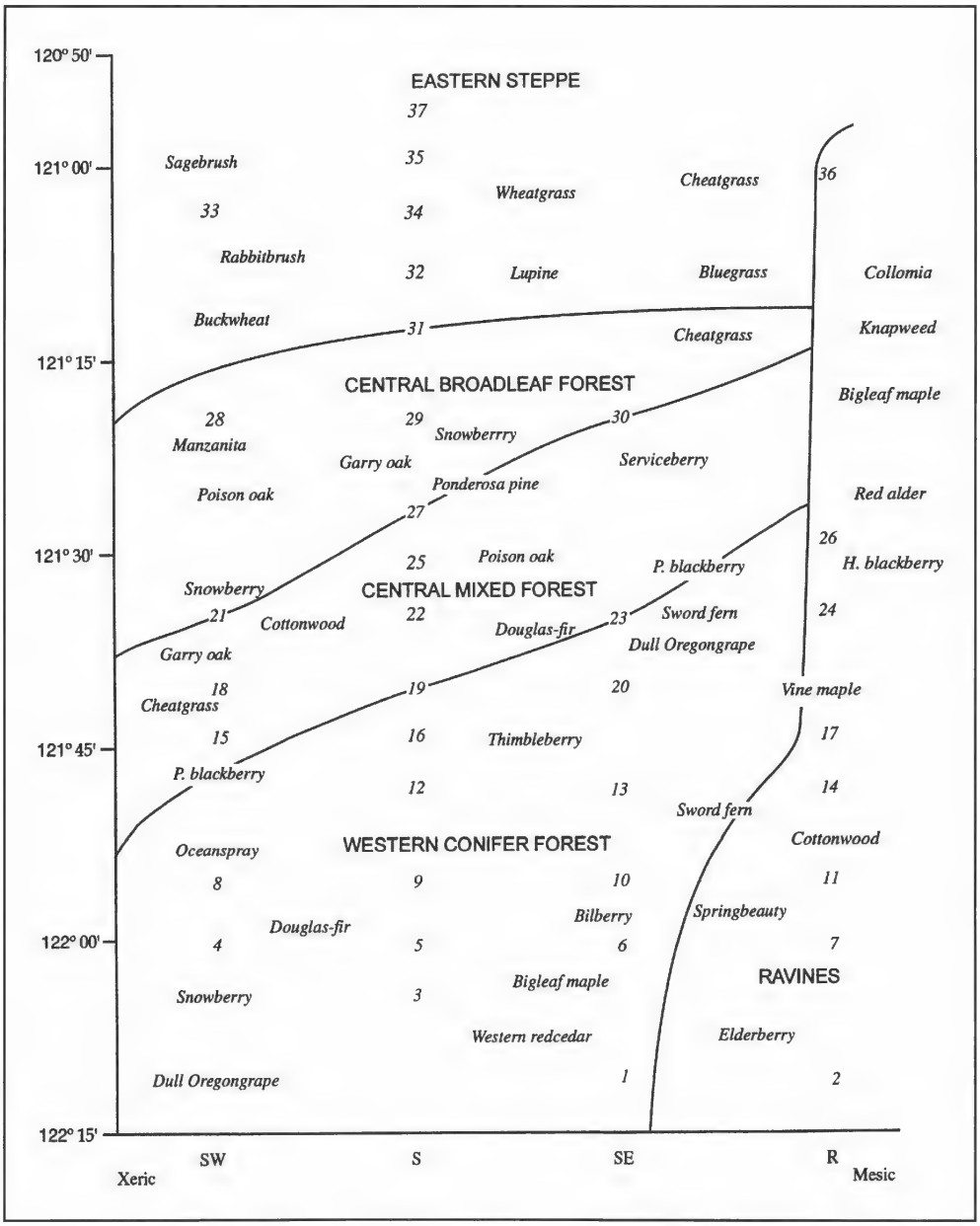

Figure 3. Mosaic diagram of environment, species, and associations on the north wall of the CRG. Major species are indicated by their centers of distribution and ranges on the north wall. Numbers 1-37 indicate the locations of the 37 macroplots.

TABLE 3. Mean density (D: trees/ha) and basal area (BA: m^2/ha) for tree species in the four associations, by topographic position. Calculations to derive association means did not use ravine data.

	Association mean		Southwest slope		South slope		Southeast slope		Ravine	
	D	BA	D	BA	D	BA	D	BA	D	BA
Western conifer forest										
Douglas-fir	361	43.4	415	36.1	338	44.7	362	45.0	180	21.1
Bigleaf maple	112	3.4	115	4.1	118	3.5	104	2.9	114	5.7
Red alder	46	0.5	65	0.7	56	0.7	28	0.2	76	2.7
Western redcedar	33	4.1	-	-	18	0.3	60	9.5	34	4.6
Ponderosa pine	21	2.3	-	-	-	-	50	5.6	-	-
Grand fir	13	0.2	-	-	10	0.1	20	0.5	14	0.2
Garry oak	7	0.8	-	-	10	1.8	8	0.1	6	1.0
Western hemlock	11	0.4	-	-	-	-	26	1.1	28	0.8
Black cottonwood	10	0.1	-	-	22	0.2	2	<0.1	14	0.2
Oregon ash	-	-	-	-	-	-	-	-	14	0.1
Soft-leaved willow	-	-	-	-	-	-	-	-	4	<0.1
Central mixed forest										
Garry oak	260	10.1	420	6.9	205	15.1	-	-	-	-
Ponderosa pine	156	13.6	100	11.0	222	18.7	60	2.8	-	-
Douglas-fir	120	6.5	110	3.3	110	6.3	190	16.6	120	3.9
Bigleaf maple	38	0.4	7	<0.1	33	0.6	150	0.8	80	10.3
Red alder	38	0.3	20	0.1	53	0.6	30	0.1	180	0.2
Black cottonwood	28	0.2	30	0.1	33	0.4	-	-	30	0.1
Lodgepole pine	21	0.7	10	0.2	30	1.1	20	0.5	-	-
Grand fir	-	-	-	-	-	-	-	-	10	0.2
Soft-leaved willow	4	<0.1	10	<0.1	-	-	-	-	20	0.1
Oregon ash	-	-	-	-	-	-	-	-	60	0.4
Central broadleaf forest										
Garry oak	230	12.2	330	14.6	195	11.8	200	10.7	100	3.1
Ponderosa pine	55	3.2	160	11.5	30	0.7	-	-	30	2.4
Bigleaf maple	15	0.4	60	1.6	-	-	-	-	170	12.1
Soft-leaved willow	15	0.2	60	0.7	-	-	-	-	-	-
Black cottonwood	-	-	-	-	-	-	-	-	80	1.0
Eastern steppe										
Bigleaf maple	-	-	-	-	-	-	-	-	70	17.8
Garry oak	-	-	-	-	-	-	-	-	20	6.2
Black cottonwood	-	-	-	-	-	-	-	-	10	4.1

circinatum), red bilberry (*Vaccinium parvifolium*), and dull Oregongrape accounted for most of the cover (Table 4). All were contagiously distributed (Whittaker 1975), with ~40-70% frequency, and they had abundant cover on all slopes. The remaining species were minor. Cover for any of them was ≤13%, frequency generally was 10-30%, and individual values varied by topographic position. As with the trees, southwest slopes supported the fewest understory species, and southeast slopes supported the most (Table 4).

Central Mixed Forest Association

The central CRG (121° 40' to 121° 25' longitude; Figure 3) supported a mixed forest with approximately equal densities of conifer and broadleaf trees, but dramatically lower overall basal area compared to the western conifer forest (Table 3). Basal area for broadleaf trees was only 34% of the conifers. Mean densities for Douglas-fir and ponderosa pine were slightly higher than for Garry oak. Douglas-fir and ponderosa pine were more

TABLE 4. Mean percent cover and frequency for shrub, forb, and grass species, and total species, in the four associations, for species with ≥5% cover in the association under consideration. SW, S, SE, R = southwest, south, southeast, and ravine.

	Cover				Frequency			
	SW	S	SE	R	SW	S	SE	R
Western conifer forest (42 species)								
Sword fern	36	16	30	26	62	28	55	46
Vine maple	36	21	19	19	56	32	33	33
Red bilberry	19	9	13	14	42	20	32	27
Dull Oregongrape	34	6	15	6	68	16	31	12
Pacific blackberry	8	8	11	4	32	27	44	11
Oceanspray	9	13	8	6	14	23	18	11
Himalayan blackberry	2	9	2	13	2	14	4	27
Thimbleberry	4	7	6	2	14	14	14	4
Snowberry	1	12	8	7	2	24	21	14
Poison oak	-	11	5	4	-	19	18	10
Bracken	8	4	2	2	28	14	13	9
Springbeauty	-	1	<1	5	-	4	2	15
Salal	-	1	5	-	-	1	12	-
Eastern red elderberry	-	-	-	8	-	-	-	17
Central mixed forest (38 species)								
Poison oak	27	27	10	2	52	57	16	12
Snowberry	12	20	23	-	21	34	48	-
Cheatgrass	38	28	-	-	73	68	-	-
Dull Oregongrape	8	8	16	-	17	24	28	-
Sword fern	-	2	24	17	-	2	40	32
Pacific blackberry	<1	7	7	7	1	24	28	28
Tall Oregongrape	7	4	-	-	16	9	-	-
Bluebunch wheatgrass	4	8	-	-	12	20	-	-
Wyeth's lupine	5	-	-	-	13	-	-	-
Maidenhair fern	-	-	-	9	-	-	-	16
Thimbleberry	-	-	-	8	-	-	-	12
Wall lettuce	-	-	-	6	-	-	-	32
Cow-parsnip	-	-	-	5	-	-	-	8
Central broadleaf forest (30 species)								
Cheatgrass	31	49	59	49	96	96	92	76
Poison oak	25	9	-	11	56	24	-	16
Western serviceberry	14	7	11	-	40	16	24	-
Sandberg's bluegrass	5	6	4	-	52	42	32	-
Squaw currant	2	6	7	-	8	14	16	-
Snowberry	5	-	-	4	12	-	-	4
Oceanspray	8	-	-	-	8	-	-	-
Arrowleaf balsamroot	4	9	-	-	20	28	-	-
Bristly manzanita	10	-	-	-	40	-	-	-
Wyeth's lupine	-	9	-	-	-	30	-	-
Mockorange	-	-	10	4	-	-	16	8
Spotted knapweed	-	-	5	12	-	-	40	52
Gray's lomatium	-	-	7	-	-	-	16	-
Eastern steppe (22 species)								
Cheatgrass	50	48	-	54	96	93	-	88
Northern buckwheat	14	7	-	-	40	23	-	-
Gray rabbitbrush	9	2	-	-	16	4	-	-
Big sagebrush	6	2	-	-	12	3	-	-
Mockorange	4	-	-	8	4	-	-	8
Wyeth's lupine	-	12	-	-	-	31	-	-
Sandberg's bluegrass	-	4	-	8	-	20	-	32
Bluebunch wheatgrass	-	5	-	-	-	19	-	-
Large-flowered collomia	-	-	-	28	-	-	-	52

important on southeast and south slopes, and this association supported the highest mean density of ponderosa pine. In contrast, Garry oak was more prominent on southwest slopes, often as dense stands of dwarfed trees, but was absent on southeast slopes (Table 3). The seven other tree species in this association were minor, except bigleaf maple on southeast slopes.

The sparse understory in the central mixed forest was dominated by poison oak. Except for cheatgrass on southwest slopes, however, no species reached 30% cover (Table 4). Poison oak and snowberry were distributed across all slope aspects, often contagiously with 30-50% frequency. Cheatgrass was prominent on southwest and south slopes, with ≥65% frequency, but absent from southeast slopes. Prominent species from the western conifer forest had dramatically different cover and frequency in the central mixed forest. For instance, in the central mixed forest, maximum mean cover for sword fern (24%) was lower than overall mean cover (36%) in the western forest. Dull Oregongrape mean cover was ~75% less on southwest slopes (Table 4). Vine maple and red bilberry were absent. Conversely, bluebunch wheatgrass (*Agropyron spicatum*) and Wyeth's lupine (*Lupinus wyethii*), abundant in the Columbia Basin, were sparse in central mixed forests. In general, the low frequencies indicate that understory species were distributed more irregularly in the central mixed forest than in the western conifer forest.

Central Broadleaf Forest Association

The central broadleaf forests extended from 121° 25' to 121° 10' longitude (Figure 3). These stands, strongly influenced by the drier climate in the eastern CRG (Table 2), supported low tree densities. Garry oak dominated, but all other species averaged well below 100 trees/ha on every slope aspect in this region (Table 3). Southeast slopes supported only Garry oak in the canopy. Ponderosa pine was the only prominent conifer, especially on southwest slopes that supported some sizeable trees (Table 4). The other three species were minor, and this region was beyond the tolerance range of Douglas-fir. The character of the forest was set more by broadleaf trees than by conifers.

The understory of the central broadleaf forest was a mixture of species from the central mixed forest and eastern shrub steppe, but total cover here was sparser than in the two forest associations to the west. Cheatgrass clearly dominated across all slope aspects, with mean cover >30% and high frequency (Table 4). Poison oak was an important associate on southwest and south slopes, and western serviceberry (*Amelanchier alnifolia*) was subordinate on all slope aspects (Table 4). Both species were clumped in the cheatgrass matrix. Sandberg's bluegrass (*Poa sandbergii*) had relatively high frequency, but this low-statured plant contributed little overall cover (Table 4). Otherwise no other species was consistently distributed throughout the region. Cover of these subordinate species was ≤10%, and frequency seldom exceeded 30%.

Eastern Steppe Association

This dry, treeless association extended east of Horsethief Lake at 121° 10' longitude (Figures 1, 3). Structurally, the stands in this region of the CRG were similar to the Columbia Basin shrub-grass steppe (Daubenmire 1970), characterized by broad expanses of grasslands through which contagiously grouped perennials were scattered. The eastern steppe is distinguished by hot summers and cold winters (Table 1), and it has the lowest precipitation of any association in the CRG (Table 2). No southeast slopes in this portion of the CRG met our sampling criteria. Southwest and south slopes were dominated by cheatgrass, with mixtures of other steppe species, none of which reached 15% cover (Table 4). Cheatgrass was uniformly distributed with high cover in the eastern steppe. Notable subordinates were northern buckwheat (*Eriogonum compositum*) on southwest slopes and Wyeth's lupine on south slopes. Gray rabbitbrush (*Chrysothamnus nauseosus*), big sagebrush (*Artemisia tridentata*), and mockorange (*Philadelphus lewisii*) provided sparse shrub cover (Table 4). None of these woody species exceeded 16% frequency.

Ravines

Species composition and community structure in the ravines in the western conifer forests were similar to the southeast slopes, but less similar to south and southwest slopes (Tables 3, 4). Bigleaf maple density in the ravines equaled or exceeded density on the slopes. Douglas-fir density and basal area were 40-50% compared to the slopes. Eight

other species on southeast slopes were present as subordinates in the ravines, although densities varied slightly. Oregon ash was present in the CRG only in ravines in the western and central forests (Table 3).

Ravines in the central mixed forest association had a strong broadleaf character. Compared to nearby slopes, red alder density increased dramatically; Garry oak, ponderosa pine, and lodgepole pine (*Pinus contorta*) were absent (Table 3). Bigleaf maple, Oregon ash, and soft-leaved willow were important subordinates. Black cottonwood (*Populus trichocarpa*) density was greater than in western ravines. Ravines in the central CRG supported fewer trees/ha than ravines in the western CRG. This trend toward broadleaf dominance continued eastward. Ponderosa pine was minor in ravines in the central broadleaf forests, and no conifers grew in the ravines in the eastern steppe (Table 3). Bigleaf maple was the dominant canopy species in the eastern ravines, with a few Garry oaks and black cottonwoods (Table 3).

Compared to the canopy layer, understory differences in the ravines were less distinct than on the slopes. In the western conifer forests, sword fern, vine maple, and red bilberry clearly dominated ravine understories, as on the slopes (Table 4). The only species absent from the western ravines was salal (*Gaultheria shallon*). The alien Himalayan blackberry was abundant in the western conifer ravines, but minimal on the slopes, in contrast to the native Pacific blackberry (*Rubus ursinus*). In the central mixed forest, only six species had ≥5% mean cover, and no species had >35% frequency (Table 4). In the central broadleaf forests and eastern steppe, cheatgrass dominance on the slopes was maintained in the ravines. Few species grew in ravines in the eastern portions of the CRG, but the alien spotted knapweed (*Centaurea maculosa*) was favored by ravines in the central broadleaf forest association. Knapweed ranked second in cover, and frequency was >50% (Table 4). Few forbs were present in CRG ravines. The most important forbs were western springbeauty (*Montia sibirica*) in western ravines, wall lettuce (*Lactuca muralis*), cowparsnip (*Heracleum lanatum*), and Gray's lomatium (*Lomatium grayi*) in central ravines, and large-flowered collomia (*Collomia grandiflora*) in eastern steppe ravines.

Tree species

Douglas-fir was the dominant tree species in the western and central CRG, where maximum density exceeded 300 stems/ha (Figure 4). It was excluded from only the wettest sites in the western ravines. Douglas-fir was present in the eastern forests, but was limited to south aspects, where density was <50 trees/ha (Table 3, Figure 4).

Western redcedar (*Thuja plicata*) achieved maximum density in the western conifer forest on southeast slopes and in ravines (Figure 4). This species was narrowly confined to the most mesic sites in the CRG, and it did not grow east of 121° 55'.

Geographically, the most widely distributed tree species in the CRG was bigleaf maple, which extended from the western forests at 122° 15' to the ravines of the eastern steppe at 120° 55'. It reached maximum distribution in ravines of the western conifer forest, with density of ~200 trees/ha (Figure 4). In the eastern CRG, bigleaf maple grew on mesic sites, with density of ~100 trees/ha.

Black cottonwood was distributed almost as widely as bigleaf maple, but density was consistently lower (Table 3, Figure 4). The center of cottonwood distribution was in the central CRG, where it was found on southwest and south slopes, and in ravines. Maximum density, however, was in the ravines of the central mixed forest (Table 3).

The highest density of Garry oak (>475 trees/ha) occurred in the central mixed forest and central broadleaf forest (Figure 4). The high densities for Garry oak were observed in several isolated stands, either in a savanna structure or in dwarfed stands.

Ponderosa pine was concentrated in the central mixed forest and central broadleaf forest. It reached maximum density of >200 trees/ha on the southwest slopes of the central broadleaf forest (Figure 4). Southeast slopes in the western conifer forest were within the tolerance range of ponderosa pine, but it was absent from other sites (Table 3).

Understory species

Deciduous shrubs were indiscriminately distributed throughout the CRG, on almost all aspects in each of the forest associations (Figure 5). Maximum cover was reached in the ravines in the western conifer forest for vine maple, red bilberrry,

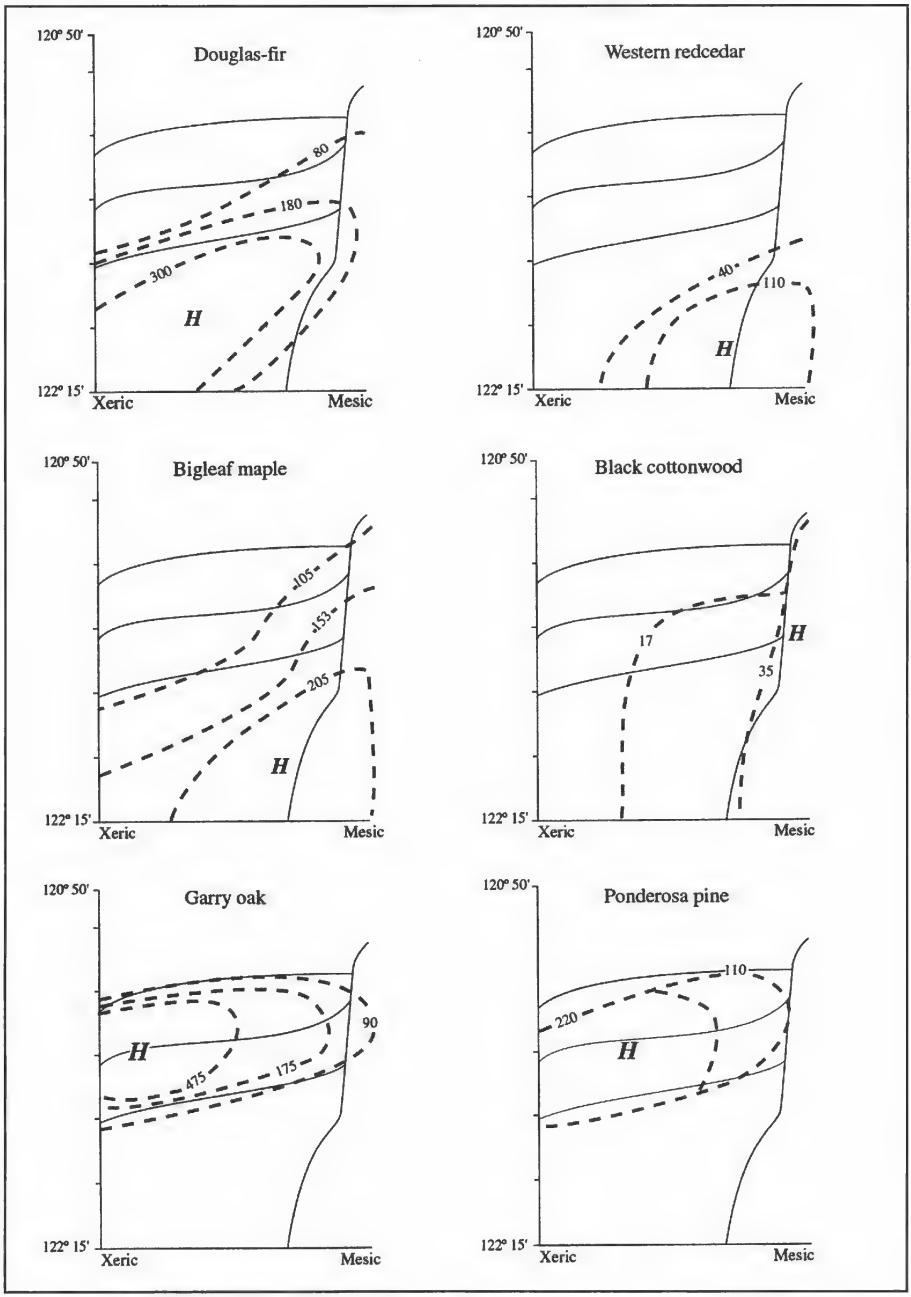

Figure 4. Distribution of important tree species on the north wall of the CRG. Values are trees/ha. H indicates maximum centers of distribution, according to actual density on the individual macroplots located on Figure 2. These diagrams are minimally connected to the mean data presented in Table 3, because they are based on measured values in specific macroplots.

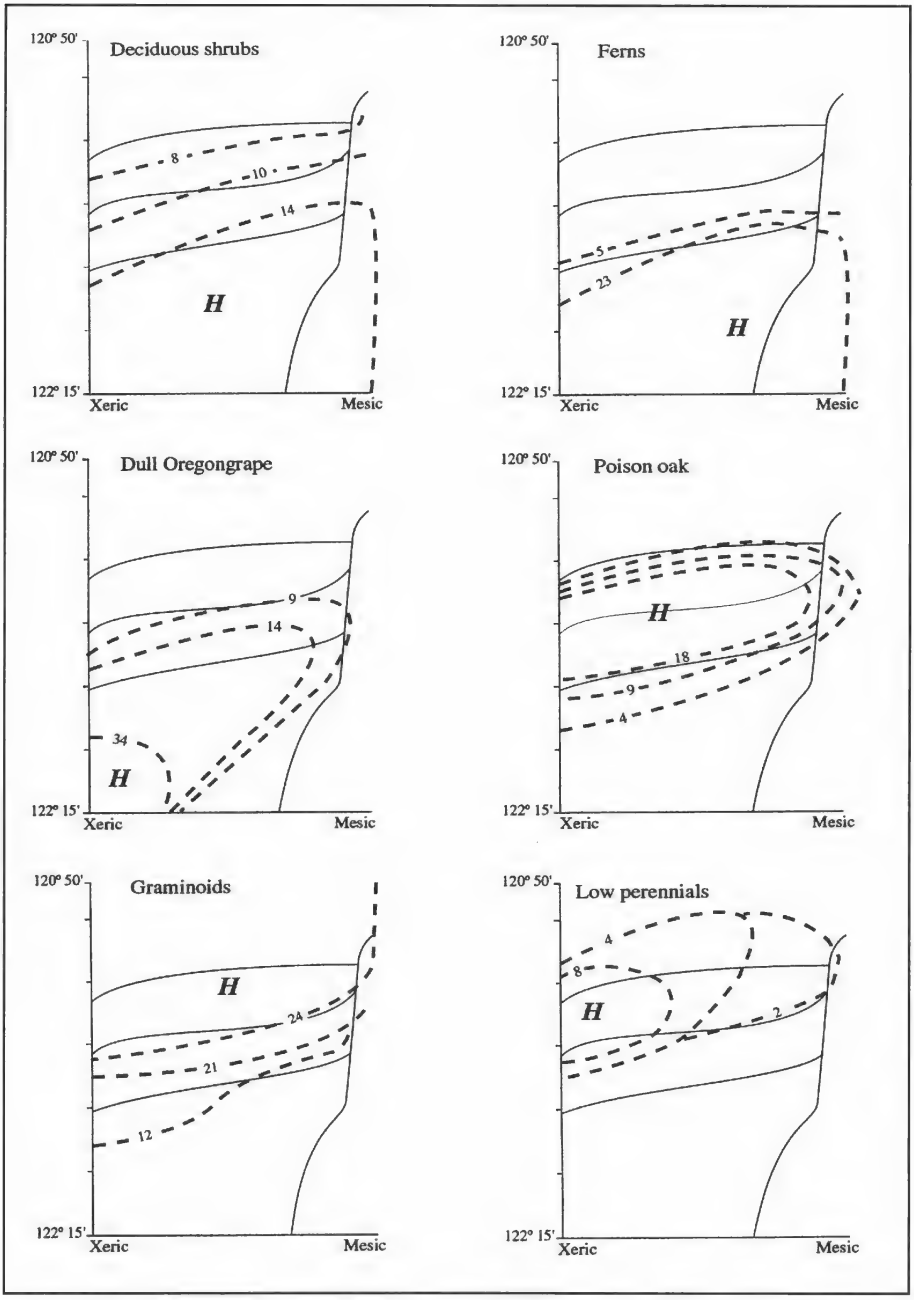

Figure 5. Distribution of important understory growth forms and species in the CRG. Values are percent cover. H indicates maximum centers of distribution, according to actual cover values on the individual macroplots located on Figure 2. These diagrams are minimally connected to the mean data presented in Table 4, because they are based on measured values in specific macroplots.

oceanspray (*Holodiscus discolor*), thimbleberry (*Rubus parviflorus*), and eastern red elderberry (*Sambucus racemosa* ssp. *pubens*). Snowberry, western serviceberry, mockorange, and squaw currant (*Ribes cereum*) extended the distribution of the deciduous shrub growth form eastward as far as the ravines in the eastern steppe (Table 3, Figure 5).

Ferns, such as sword fern, bracken (*Pteridium aquilinum*), and maidenhair fern (*Adiantum pedatum*) reached highest cover in the western conifer forest and in ravines (Figure 5). They were indiscriminate species, and occurred at high frequencies on mesic sites. Ferns extended eastward in the CRG on southeast slopes and ravines of the central mixed forest.

The distribution of dull Oregongrape (Figure 5) generally encompasses the distribution of other evergreen shrubs in the forests, including salal, tall Oregongrape (*Berberis aquilifolium*), and bristly manzanita (*Arctostaphylos columbiana*). Dull Oregongrape was a dominant understory species in the western conifer forest, reaching maximum cover on southwest slopes (Table 4). It was a broadly tolerant species, found on all aspects except ravines, although its cover was low.

Poison oak was a prominent species in the central mixed forest and the central broadleaf forest (Figure 5). The tolerance range of this shrub extended onto south slopes of the western conifer forest, and into the ravines of all three forest associations (Table 3). Poison oak was most commonly encountered in the understory of stands dominated by Garry oak, but it was not restricted to these forests.

Graminoids were widely distributed throughout the CRG, extending onto southwest slopes from the western forests to the eastern steppe (Figure 5.) The highest cover for graminoids was encountered in the eastern steppe and central broadleaf forest, where they averaged ~45% cover. The vast majority of this cover was supplied by the alien cheatgrass (Table 4). Native species, such as bluebunch wheatgrass, Sandberg's bluegrass, and Idaho fescue (*Festuca idahoensis*) accounted for little cover.

Low perennials, such as arrowleaf balsamroot (*Balsamorhiza sagittata*), northern buckwheat, and Wyeth's lupine, were found primarily in the central broadleaf forest and eastern steppe (Figure 5, Table 4). Maximum cover was on south and southwest aspects, where they combined for 12-18% cover.

Discussion

The ecocline on the north wall of the Columbia River Gorge reflects the interaction among precipitation, wind, temperature, soil moisture, and the individual tolerance ranges of plant species. Each association in the CRG supported species distributed individually along the ecocline (Figures 3, 4, 5). The centers of distribution were in the western CRG for a number of species, including Douglas-fir, western redcedar, bigleaf maple, dull Oregongrape, sword fern, bracken, vine maple, and red bilberry (Figures 4, 5). The centers of distribution for Garry oak, ponderosa pine, poison oak, and snowberry were in the central CRG (Figures 4, 5). The centers of distribution for cheatgrass, northern buckwheat, Wyeth's lupine, western serviceberry, mockorange, and Sandberg's bluegrass were in the eastern CRG (Figures 4, 5).

Although each species reached maximum distribution in one region of the CRG, few were confined to a specific geographic location or vegetation association. Douglas-fir grew eastward to 121° 20', whereas cheatgrass was present westward to 122° 05'. Garry oak grew on all aspects from 121° 45' to 121° 15', and poison oak occurred from 121° 55' to 121° 15'. Bigleaf maple was the only species with high density throughout the CRG, and cheatgrass and Wyeth's lupine also were present in all four associations. The prominent plant species in the CRG ranged well beyond their centers of distribution.

The ecocline in the CRG is a product of changes in environmental factor complexes, species distribution, and physiognomic associatons. This ecocline is similar to the Santa Catalina Mountains, Arizona, where slope aspect was superimposed on the variable mountain environment (Whittaker and Niering 1965). The CRG is analogous to a mountain turned on its side, with the cool, moist summit to the west and the warm, dry base to the east. The cooler, moister conditions in the western CRG promote the dense western conifer forest. The western conifer forests in the CRG are extensions of the regional upland forests in southwest Washington and northwest Oregon. The potential natural vegetation of this region constitutes forests dominated by Douglas-fir

in association with western hemlock, western redcedar, and bigleaf maple, with sword fern, vine maple, and dull Oregongrape prominent in the understory (Troll 1955, Habeck 1961, Franklin 1965, Detling 1958, Johannessen et al. 1971, Franklin and Dyrness 1988, Schoonmaker and McKee 1988, Brockway 1998, Bailey et al. 1998, Barbour and Billings 2000). The gradation from western conifer to central mixed forest coincided with the loss of several species adapted to mesic conditions, such as western redcedar and western hemlock, and the reduction of sword fern (Figures 4, 5).

The central mixed forest and central broadleaf forest marked the transition to a warmer and drier growing season. These drier forests were dominated by Garry oak, with mixtures of ponderosa pine (Table 3). Floristic patterns in the central broadleaf forests resembled the central mixed forests, except for the lack of conifers eastward. A similar environmental change involving pines and oaks was observed in the Klamath Mountains eastward from the Pacific Ocean (Whittaker 1961). The central mixed forest is unique in the Pacific Northwest. The nearest similar combination of species occurs in the Siskiyou Mountains of southern Oregon, where lower elevation forests on xeric slopes are dominated by mixed combinations of sugar pine (*Pinus lambertiana*), Douglas-fir, canyon live oak (*Quercus chrysolepis*), and California black oak (*Q. kelloggii*), with poison oak and dull Oregongrape prominent in the understory (Whittaker 1960). Detling (1958) previously noted the strong floristic connection between the Rogue River area and the Columbia River Gorge.

The hot, arid, windy environmental regime in the eastern CRG severely limits plant growth and diversity, and it excludes trees in favor of grasses. The vegetation of the eastern steppe is similar to the Columbia Basin, where cheatgrass, northern buckwheat, lupines, big sagebrush, and rabbitbrush are prominent (Daubenmire 1970, 1975; Cline et al. 1977; Sauer and Rickard 1979; Franklin and Dyrness 1988). The potential natural vegetation of the eastern CRG falls within the bluebunch wheatgrass-Sandberg's bluegrass zone (Daubenmire 1970), however, it is unlikely that this pattern will ever return to the CRG given the current prominence of the alien cheatgrass in the eastern CRG.

The CRG is the only near sea level corridor through the Cascade Range from California to British Columbia, and plant species have migrated between the Columbia Basin and the Willamette Valley via the Gorge for millennia (Lawrence 1939, Franklin and Dyrness 1988). Movement historically has been primarily from east to west, with aridly adapted species invading new habitats, sometimes as far west as Cape Horn (Detling 1958), 12 km east of Washougal in the western conifer forest. The warmer and drier soils caused by greater insolation on the north wall have allowed steppe species, such as northern buckwheat, and Wyeth's lupine, to migrate from the Columbia Basin westward along the Columbia River (Lawrence 1939, Detling 1958). Two species important to this study, bigleaf maple and Garry oak, have migrated from west to east in the CRG (Lawrence 1939). They have been particularly successful in ravines (bigleaf maple) and xeric slopes (Garry oak) of the CRG.

In recent decades alien species have begun to migrate into and through this corridor. The most widespread alien species in the CRG, cheatgrass, has extended from the Columbia Basin to plot 1, at Cape Horn in the westernmost part of our study area (Figure 3). Cheatgrass occurred on 21 plots, and dominated the low layer of many of the plots in the eastern CRG. Cheatgrass PV on plot 18 (576), on the southwest slope of Dog Mountain, was exceeded only by plot 35 (942) in the eastern steppe association.

Himalayan blackberry occurred on 13 plots, mainly in the western CRG, and extended east as far as plot 27. Maximum PV for Himalayan blackberry came on plot 17 (202) and plot 3 (179).

The other alien species in the CRG were more narrowly distributed, and were less prominent. Wall lettuce grew on four plots (#1, 8, 12, 24) in the western conifer forest, and spotted knapweed grew on two plots (#26, 30) in the central portion of the CRG. Scot's broom (*Cytisus scoparius*) never achieved sufficient cover to be included in Table 3, but it occurred on three plots (#12, 26, 27) in the central portion of the CRG. We recorded 10 other alien species, all with low cover and frequency: hairy vetch (*Vicia villosa*), Tangier peavine (*Lathyrus tingitanus*), herb Robert (*Geranium robertianum*), filaree (*Erodium cicutarium*), dogtail (*Cynosurus echinatus*), Viper's bugloss (*Echium vulgare*), Jim Hill mustard (*Sisymbrium altissimum*), St. John's

wort (*Hypericum perforatum*), and orchard-grass (*Dactylis glomerata*).

The distribution of Garry oak and ponderosa pine in the CRG illustrates the important environmental differences between the north and south walls of the Gorge. Ponderosa pine dominates extensive forests on the east slope of the Cascade Mountains, and it is a dominant species on the Oregon side of the central and eastern CRG (Lawrence 1939). Although present in the three forest associations on the north wall of the CRG, ponderosa pine at best was a strong subordinate in the central mixed forest. The highest pine densities were on south slopes in the central mixed forest, and on southwest slopes in the central broadleaf forest, yet either Douglas-fir or Garry oak dominated the stands (Table 3). No pure oak stands exist on the Oregon side of the CRG (Lawrence 1939), yet on the Washington side Garry oak accounted for a larger percentage of total tree density, dominated many slope aspects, occurred with much greater frequency, and extended much farther west than isolated oaks on the south wall. Oaks in the north wall forests typically were smaller than those on the south wall, which grow farther east beyond the limits of the CRG (Lawrence 1939).

Acknowledgements

We are pleased to thank the National Forest Service and Washington State Parks for permission to sample on their lands. Mary Wolter, Bill Wolter, and Cheryl Gray assisted with the field work, and Jeannie Gilbert created Figures 1-5. We are grateful for their help.

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Received 11 December 2000
Accepted for publication 19 September 2001

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Northwest Science Notes

The purpose of "Notes" is to periodically publish short papers (typically less than five pages in length). There is no specific format or content required for articles published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

Stephen R. Goldberg,[1] Department of Biology, Whittier College, Whittier, California 90608

Charles R. Bursey, Department of Biology, Pennsylvania State University, Shenango Campus, Sharon, Pennsylvania 16146

and

Cheryl Wong, Department of Biology, Whittier College, Whittier, California 90608

Helminths of the Western Chorus Frog from Eastern Alberta, Canada

Abstract

Western chorus frogs from eastern Alberta, Canada were examined for helminths. Two species of trematode (*Apharyngostrigea pipientis* and *Choledocystus pennsylvaniensis)*, one species of cestode (*Cylindrotaenia americana)* and two species of nematode (*Oswaldocruzia leidyi* and *Rhabdias ranae)* were found. The western chorus frog represents a new host record for *A. pipientis*. Alberta, Canada, represents a new locality record for each species of helminth found in this study.

Introduction

The western chorus frog (*Pseudacris triseriata* [Wied-Neuwied, 1838]: Hylidae) occurs from Great Bear Lake, Northwest Territories, Canada to central Ontario, Canada south to Georgia and the Texas Gulf Coast and west to central Arizona at elevations from near sea level to 3670 m (Stebbins 1985). It is found throughout Alberta except in alpine habitats (Russell and Bauer 1993). There are reports of helminths in western chorus frogs from Ontario (Adamson 1981; Baker 1977, 1978; Vanderburgh and Anderson 1987), Arizona (Goldberg et al. 1996), Colorado (Ubelaker et al. 1967), Indiana (Whitaker 1971), Iowa (Ulmer 1970), Michigan (Muzzall and Peebles 1991), Nebraska (Brooks 1976), Ohio (Ashton and Rabalais 1978; Odlaug 1954), Texas (Harwood 1932), and Wisconsin (Bolek and Coggins 1998). The purpose of this note is to report helminths found in western chorus frogs from eastern Alberta, Canada.

[1] Author to whom correspondence should be addressed. E-mail: sgoldberg@whittier.edu

Methods

Thirty-eight preserved adult specimens of western chorus frogs (mean snout-vent length [SVL] = 25.1 mm ± 0.4 SE) were borrowed from the Museum of Zoology, Department of Zoology, University of Alberta, Edmonton (UAMZ) for helminthological examination. Seventeen female (snout-vent length, SVL = 25.9 mm ± 0.6 SE) and 21 male (SVL = 24.5 mm ± 0.4 SE) frogs were examined. These specimens had been collected in 1950, 1951, and 1968 from eastern Alberta within the area bounded by 49°39'-53°36'N and 110°00'-114°35'W. Accession numbers are: UAMZ 129, 133, 184-186, 233-235, 264, 373-376, 387, 387.1-387.17, 423-425, 455, and 1722-1724.

The frogs had been fixed in 10% formalin and preserved in 70% ethanol. We opened the body cavity, removed the gastrointestinal tract by cutting across the esophagus and rectum and examined the stomach, small intestine, large intestine, body cavity, liver, lungs, and urinary bladder using a dissecting microscope. Nematodes were placed on a glass slide, cleared in undiluted glycerol, and identified using a compound microscope.

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TABLE 1. Helminths of the western chorus frog from eastern Alberta, Canada.

Helminth species	Site of infection	Prevalence (%)	Mean intensity ± SE	Range	Abundance
Trematodes					
Apharyngostrigea pipientis[1]	kidney	8	5.7 ± 2.0	2-9	0.45
Choledocystus pennsylvaniensis	small intestine	21	11.3 ± 4.3	1-35	2.37
Cestodes					
Cylindrotaenia americana	small intestine	3	3.0	3	0.08
Nematodes					
Oswaldocruzia leidyi	stomach, small intestine	11	3.0 ± 0.9	1-5	0.32
Rhabdias ranae	lung	3	1.0	1	0.03

[1]new host record

Selected cestodes and trematodes were regressively stained with hematoxylin, cleared in xylene, and mounted in balsam for identification using a compound microscope.

Results

Adults of two trematode species, *Apharyngostrigea pipientis* (Faust, 1918) Olivier, 1939 and *Choledocystus pennsylvaniensis* (Cheng, 1961) Byrd and Maples, 1963; one cestode species, *Cylindrotaenia americana* Jewell, 1916; and two nematode species, *Oswaldocruzia leidyi* Travassos, 1917 and *Rhabdias ranae* Walton, 1929 were found. Each helminth species was categorized according to the following criteria (Table 1):

- Prevalence: number of individuals of a host species infected with a particular parasite species divided by the total number of hosts examined and expressed as a percentage;
- Mean intensity: summation of individuals of a particular parasite species in a sample of a host species divided by the number of infected hosts;
- Range: minimum to maximum number of individuals of a particular parasite species in a sample of host species;
- Abundance: total number of individuals of a particular parasite species in a sample of hosts divided by the total number of hosts in the sample;
- Infection site: anatomical position of parasite species within host.

There was no significant difference in SVL between female and male frogs (Kruskal Wallis test = 3.64, 1 df, $P > 0.05$). Thirteen (34%) of 38 frogs harbored 123 helminths. Nine frogs harbored one helminth species and four frogs harbored two helminth species. There was no significant difference in overall infection rate between female and male frogs. The mean number of helminth species per infected host, mean number of helminth individuals per infected host and overall helminth abundance were 1.3 ± 0.1 SE, 9.5 ± 2.7 SE, and 3.2 ± 1.2 SE. The trematode *Choledocystus pennsylvaniensis* had the highest prevalence, mean intensity, and abundance of all helminths in this sample of western chorus frogs.

Selected specimens of the following helminths were placed in vials of 70% ethyl alcohol, deposited in the United States National Parasite Collection, (USNPC) Beltsville, Maryland, and assigned the following accession numbers: *Apharyngostrigea pipientis* (metacercaria) (90116), *Choledocystus pennsylvaniensis* (90117), *Cylindrotaenia americana* (90118), *Oswaldocruzia leidyi* (90119), *Rhabdias ranae* (90120).

Discussion

A list of reported parasites for the western chorus frog was provided by Bolek and Coggins (1998). To that list should be added the reports by Harwood (1932) of *Cylindrotaenia americana, Brachycoelium salamandrae* (= *B. daviesi*) and *Megalodiscus temperatus,* and by Ulmer (1970) of *Fibricola cratera*. Our report of *Apharyngostrigea pipientis*, *Choledocystus pennsylvaniensis* (=*Glypthelmins pennsylvaniensis*), *Cylindrotaenia americana, Oswaldocruzia leidyi*, and *Rhabdias ranae* should also be added to that list. The western chorus frog represents a new host record for *Apharyngostrigea pipientis*. Alberta, Canada, represents a new locality record for each species of helminth found in this study.

It appears from the parasite list that the western chorus frog is infected by a variety of generalist helminths that infect a number of host species. We concur with Bolek and Coggins (1998) that treefrog helminths are not host specific.

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Received 10 May 2001
Accepted for publication 17 August 2001

Acknowledgements

We thank Wayne Roberts, Collections Manager (Department of Zoology, University of Alberta) for permission to examine specimens of the western chorus frog.

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D. E. Hibbs,[1] Department of Forest Science, Oregon State University, Corvallis, Oregon 97331

M. V. Wilson, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

and

A. L. Bower, Department of Forest Science, Oregon State University, Corvallis, Oregon 97331

Ponderosa Pine of the Willamette Valley, Western Oregon

Abstract

Ponderosa pine is an overlooked component of the historical vegetation in the Willamette Valley of western Oregon. Pollen, historical, and field data show that ponderosa pine has been a component of both lowland/floodplain and upland/foothill vegetation. In the latter, it was an important constituent of the savanna and open oak woodland vegetation that was widespread in the early 1800s. Much of the historical range of ponderosa pine has been converted to other land uses, such as agriculture, or changed by ecological succession to a closed forest dominated primarily by Douglas-fir. Efforts to understand past Willamette Valley vegetation or to restore historical ecosystems in the Valley should recognize the important ecological position once held by ponderosa pine.

Introduction

Most residents of the Willamette Valley of western Oregon do not recognize ponderosa (yellow) pine (*Pinus ponderosa*) as a natural part of their landscape. Most assume that the scattered ponderosa pine seen in the Valley were grown from seed collected east of the Cascade Mountains. In fact, some standard references (Franklin and Dyrness 1973) do not mention ponderosa pine occurring in the Valley north of Eugene. Thus, many are surprised to learn that ponderosa pine has been growing throughout the Willamette Valley for several thousand years (Pearl 1999) and that it is a genetic race distinct from the ponderosa pine found east of the Cascade Mountains (Gooding 1998)

Because of the increasing interest in ecological restoration and in establishment of ponderosa pine timber plantations in the Willamette Valley, we investigated the past and present distribution of ponderosa pine to develop a fuller understanding of its ecological requirements and successional position within the Valley. This paper presents a review of the literature on ponderosa pine, augmented with data we collected south of Eugene.

[1]Author to whom correspondence should be addressed; E-mail david.hibbs@orst.edu

Prehistoric Ponderosa Pine

Sediment cores from Lake Labish and Onion Flats, two neighboring deep peaty deposits in the central Willamette Valley (Figure 1), revealed the presence of pine (Hansen 1947). Although this study predated ^{14}C dating techniques, the chronology of the cores can be tied to the Mazama pumice deposit of about 6800 years before present (ybp). Pine was more abundant toward the bottom of the cores, declined to very low levels, then increased in abundance around 7000 ybp (just above the Mazama ash layer) to levels it maintained to the present. Dated sediment cores from an old ox-bow of the Willamette River near Albany (Pearl 1999) showed abundant pine pollen toward the bottom of the core at 11,000 ybp, declining to very low levels around 10,000 ybp, and rising slightly to the current low levels around 7,000 ybp. Many of the current Willamette Valley prairie and woodland species also became common in the pollen profiles around 7,000 ybp.

Interpretation of these pollen data is complicated because the pollen of ponderosa pine cannot be distinguished from lodgepole pine (*Pinus contorta*). Current ecological requirements of these species (Franklin and Dyrness 1973, Burns and Honkala 1990) and changes in community types depicted by the pollen cores (Pearl 1999) and concomitant climate change (Whitlock 1992)

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suggest that the pollen of 8,000 ybp and older is lodgepole pine (Hansen 1967) and that pine pollen deposited in the Willamette Valley in the last 7,000 years is ponderosa pine.

Ponderosa Pine Before 1850

Historical Records

Early accounts of the Valley provide anecdotal evidence of ponderosa pine. The journal of David Douglas (Davies 1980) described an oak-pine savanna in the north Valley near present-day Newberg (Figure 1). Douglas described pines growing in the foothills of the western and southern parts of the Valley. An unnamed missionary described groves of oak and pine near Salem in 1840 (Smith 1949). A sawmill built in 1852 south of Alpine processed pine cut from a stand near Monroe (Figure 1) (Anonymous 1942).

The historic vegetation distribution of ponderosa pine in western Oregon can be investigated

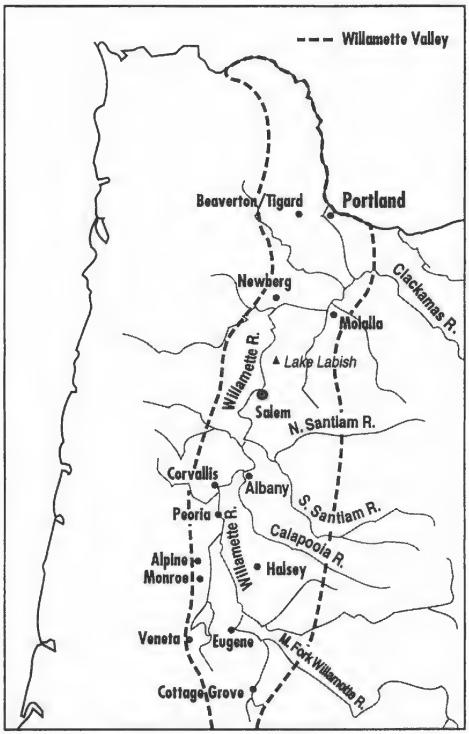

Figure 1. The Willamette River Valley, noting locations cited in the text.

through the 1852-53 General Land Office (GLO) survey records. The GLO survey identified witness trees at each section and half-section corner by species and mapped vegetation boundaries. The survey records provide an unusually systematic description of vegetation at the time. The GLO records mention ponderosa pine with white oak (*Quercus garryana*) and sometimes Douglas-fir (*Pseudotsuga menziesii*) on the foothills, on the flood plain, and in riverine forests between Eugene and Halsey (Johannessen et al. 1971), near the Willamette River adjacent to Monroe where they were subject to inundation (Benner and Sedell 1997), and with Oregon white oak and Douglas-fir in grass northeast of Eugene (Boag 1992). Most of the pine was on the lower hills at the sides of the Valley (Johannessen et al. 1971, Boag 1992). On the prairie-dominated flood plain, isolated oaks, pines and Douglas-firs grew under special conditions created by former dwellings, thin soil and rock outcrops (Johannessen et al. 1971).

These direct accounts in the GLO records confirm the presence of ponderosa pine throughout much of the Willamette Valley. Ponderosa pine was not mentioned in Habeck's (1961) transect across the Valley at Salem and in Towle's (1982) transect at Monroe (where two other studies above mention pine), suggesting that ponderosa pine was not abundant in their study areas or was considered unimportant by these researchers.

The historical distribution of ponderosa pine can also be inferred from sources other than the GLO surveys. In a study of the Fox Hollow Research Natural Area, an unlogged area immediately south of Eugene, Cole (1977) found that Douglas-fir was the most common tree species before 1850. Ponderosa pine and white oak were common associates on the hilltop and upper southerly slope, where 23%–29% of the 64–70 trees per ha was ponderosa pine. A small amount of incense cedar (*Calocedrus decurrens*) was also present. Thus, this site in 1850 had a scattering of trees on an open hillside, with ponderosa pine as an important component.

These reports collectively suggest that ponderosa pine was widely distributed in the Willamette Valley before 1850. Ponderosa pine occurred in an open forest with combinations of oak and Douglas-fir on sites from the occasionally flooded valley bottoms to very well-drained hills. We found little record of ponderosa pine in

the prairie zone or in the river-related bottomland hardwood type.

Stand Reconstruction Study

We conducted a stand reconstruction study on Bureau of Land Management property in two 16-ha unlogged stands near the Fox Hollow RNA south of Eugene (sections 11 and 21 of T19S, R4W). We first surveyed each stand for old ponderosa pine. The stand in section 11 contained nine ponderosa pine trees, six of which pre-dated 1850. All were located in a north-south line on the west face of the hill, just below the top. A visual survey detected only 4–9 other trees that appeared to pre-date 1850 on the basis of bark, branch and stem characteristics, although there were a few dead open-grown white oaks of indeterminate dates of origin on the upper west slope. The stand in section 21 contained six ponderosa pine trees arranged roughly in pairs, as well as Douglas-fir and incense cedar that appeared to pre-date 1850. The older trees tended to be near the top of two west-facing ridges, not low on slopes or near the intervening stream.

We selected seven ponderosa pine trees from the two stands to serve as focal trees for further sampling. We mapped the location of immediately adjacent codominant and subdominant neighbors. We aged the focus pine and a sample of the adjacent trees by counting annual rings, adjusting age for height of the increment core or section. Six of the eight ponderosa pine trees in our sample (seven focus trees and one neighbor) originated before 1850 (1741, 1792, 1817, 1820, 1820, and 1835). In contrast, only six of 26 trees of other species that were codominant or subdominant canopy neighbors originated before 1850 (1677, 1773, 1795, 1801, 1808, and 1817); all were Douglas-fir.

We also sampled from three fixed-area plots (0.14 ha) centered on ponderosa pine trees in the section 21 stand. Three ponderosa pine and 31 Douglas-fir trees of the 131 trees in these plots originated before 1850 (Table 1). There was no evidence (stumps, logs, or snags) of a lost presettlement oak component in this stand, and little evidence in either stand of conifers that were canopy size in 1850 but had since died.

These results suggest that in 1850, the study area varied from ponderosa pine-Douglas-fir-oak savanna, to open woodland, to patches of closed-canopy forest. Judging by the surviving trees, the trees of the study were generally quite young in 1850 (median age = 30 yr).

TABLE 1. Total number of individuals per hectare by species in three 0.14 ha circular plots centered on ponderosa pine in the section 21 stand. The ponderosa pine originating before 1850 were focus trees. Note that these density values should not be extrapolated to the whole 16 ha of the stand. There were only 6 ponderosa pines trees in the stand, and their distribution was strongly clumped.

Species	Origin		Regeneration (<15 cm dbh)
	Before 1850	After 1850	
Ponderosa pine	7	2	2
Douglas-fir	74	86	119
Incense cedar	0	100	81
Grand fir	0	33	93
Black oak	0	7	7
Chinquapin	0	0	93
Bigleaf maple	0	0	2
Red alder	0	0	2

Ponderosa Pine Since 1850

A few studies have examined modern distribution of ponderosa pine. Hansen (1947) reported seeing sizable pine stands in the central Valley in 1938; his photos of these stands appear to be of flat sites, not hillsides. Hansen also noted that ponderosa pine grew on the outwash plains southwest of Puget Sound and in the southern Willamette Valley. Ponderosa pine was mapped in western Oregon from Portland south through the Willamette Valley to the California border (Anderson 1938). In the central Willamette Valley, he noted the highest concentration of pine was in the same flood plain area identified by Johannessen et al. (1971) and Benner and Sedell (1997).

A community analysis of closed oak stands in the central Valley showed four community types (Thilenius 1968). Only the poison oak (*Rhus diversiloba)* type contained any ponderosa pine, and it was rare even in this type. All of the stands in this analysis were low-lying, not on hillsides. All were closed-canopy, and all appeared to postdate 1850. Within these closed oak stands were scattered (average 17 per ha), overtopped open-grown oaks ranging from 257 to 308 years old. Thus, these stands had earlier been oak woodlands of the type described elsewhere as having contained ponderosa pine.

Franklin and Dyrness (1973) discussed the oak type in the Willamette Valley province without mention of ponderosa pine. They concluded, however, that ponderosa pine occurred south of Eugene mixed with Douglas-fir, and some incense cedar and oak, on ridges and south slopes and along some streams. Juday (1976), also working south of Eugene, described a similar upper slope pine type. Curiously, he described this as the northern limit of ponderosa pine in western Oregon.

Cole (1977) suggested that incense cedar has regenerated in large numbers on drier sites since 1850 and would replace ponderosa pine as the pine senesces. On more mesic sites, grand fir would replace the Douglas-fir that colonized the woodlands. As a result, stands open in 1850 have become closed forests today. Our stand reconstruction data (Table 1) show a similar pattern. Stand density, grand fir and incense cedar all increased over time. Most of the Douglas-fir regeneration in our data can be attributed to increased understory light caused by a recent clearcut adjacent to one of the ponderosa pines. Because we observed abundant natural ponderosa pine regeneration in recent clearcuts adjacent to our study area in section 21, we concluded that the lack of young ponderosa pine in our study stands is related to poor regeneration conditions (low light), not a lack of viable seed.

A survey from Eugene to the Columbia River by the Willamette Valley Ponderosa Pine Conservation Association (Robert McNitt, WVPPCA, personal communication) showed that ponderosa pine was found in any abundance in only three locations: the Beaverton/Tigard area, low elevation Cascade foothills sites from Molalla to Cottage Grove, and lowland sites near rivers south of Salem, with most occurring along a north-south line from Albany to Veneta. Ponderosa pine was conspicuously absent from Coast Range foothills.

These studies of contemporary conditions demonstrate that ponderosa pine occurs on both valley bottoms and hillsides. Because most studies north of Eugene were conducted in low-lying sites, they give the impression that it only occurs in such areas. The WVPPCA data show that today it also occurs on hillsides. Successional processes following fire suppression (Agee 1993) tend to reduce ponderosa pine abundance, although recent land use changes (e.g., farming, dwellings, Christmas trees) must also contribute to this reduction.

Conclusions

Efforts to restore historical vegetation in the Willamette Valley should include ponderosa pine woodlands. The current scarcity of ponderosa pine can be caused, not only by habitat loss, but also by fire exclusion that allows open woodland to be replaced through succession by closed forest. Reintroduction and long-term maintenance of ponderosa pine in the Willamette Valley will require active management to promote the open woodland conditions necessary for natural regeneration or the survival of planted seedlings.

Acknowledgements

The Eugene District of the Bureau of Land Management provided support. Sara Lipow, John Tappeiner, Donald B. Zobel, and an anonymous reviewer provided helpful reviews. This is publication 3433 of the Forest Research Laboratory, Oregon State University.

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Received 23 January 2001
Accepted for publication 24 July 2001

Sally A. Simmons,[1] Washington State University Tri-Cities, 2710 University Drive, Richland, Washington 99352

and

William. H. Rickard, Pacific Northwest National Laboratory, Retired, P. O. Box 999, Richland, Washington 99352

Plant Succession at the Edges of Two Abandoned Cultivated Fields on the Arid Lands Ecology Reserve

Abstract

How vegetation recovers from disturbances is an important question for land managers. We examined 500 m^2 plots to determine the progress made by native herbaceous plant species in colonizing the edges of abandoned cultivated fields at different elevations and microclimates, but with similar soils in a big sagebrush/bluebunch wheatgrass steppe. Alien species, especially cheatgrass and cereal rye, were the major competitors to the natives. The native species with best potential for restoring steppe habitats were sulphur lupine, hawksbeard, bottlebrush squirreltail, needle-and-thread grass, Sandberg's bluegrass, and several lomatiums.

Introduction

Plant succession on abandoned cultivated fields in the semi-arid interior Columbia River Basin of eastern Washington is a chronologically slow process (Daubenmire 1975, Rickard and Sauer 1982). Recolonization by native plants is slowed by the aggressive seedlings of alien annual plants, especially cheatgrass (*Bromus tectorum*), because alien seedlings compete with native seedlings for scarce soil water and nutrients (Harris 1967).

The Fitzner-Eberhardt Arid Lands Ecology (ALE) Reserve is a 30,000 ha tract of land located 25 km northwest of Richland in Benton County, Washington. Since the 1960s, the ALE Reserve has been free of grazing and managed as a research natural area (Franklin et al. 1972, Soll et al. 1999). Two abandoned cultivated fields well inside the boundaries of the ALE Reserve were selected as study sites. The lower field was located at 323 m elevation on a gently sloping, linear tract of land closely bounded on the long sides by ravines. In all, the field occupied about 10 ha. The entire field was cultivated between 1900 and 1943, and it was irrigated at least for a time with water taken from a nearby permanent spring.

The upper field (533 m elevation) was >100 ha. The edges of the cultivated ground in most places is limited by ravines and in one place by a change in past land ownership as marked by the remnants of a fenceline. This field was used to raise dryland wheat between 1900 and 1943. Slope and soil properties were similar on both sides of the fenceline.

The general habitat-type of both fields is big sagebrush/bluebunch wheatgrass (*Artemisia tridentata/Pseudoroegneria spicata*) as described by Daubenmire (1970). The microclimate of the upper field is slightly cooler and wetter than the lower field. Precipitation at the upper field averages 22.5 cm compared to 19.5 cm at the lower field. Average maximum January air temperature was 11.5°C at the upper field and 12.5°C at the lower field. Average maximum July air temperature at the upper field was 41.0°C compared to 44.5°C at the lower field. Average minimum January air temperature was –17.0°C at the upper field and –15.5°C at the lower field. Average minimum July air temperature at the upper field was 6.0°C compared to 8.5°C at the lower field. The soil texture at both fields is mapped as silt loam (Thorp and Hinds 1977).

Our work had three objectives: 1) analyze the vegetation on the edges of 57-yr-old abandoned fields to determine those native perennial species with the greatest propensity to recolonize the fields; 2) obtain information on species composition and abundance of native perennials on nearby unplowed ground; and 3) mark the locations of the study plots to facilitate monitoring the future progress of succession.

Methods

We elected to place study plots near the edge of the fields because the edges were closest to sources of native seeds. Two adjacent 20- by 25-m

[1]Author to whom correspondence should be addressed. Email: ssimmons@tricity.wsu.edu.

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macroplots were located 10 m inside the downslope boundary of the lower field and were labeled A and B. In the upper field, we placed one 20- by 25-m macroplot on cultivated ground and the adjacent macroplot on ground that had never been cultivated. The macroplots were separated only by the remnants of a fenceline. The uncultivated macroplot was included to show species richness and abundance of native perennial plants at a place with closely similar soil and topography near the edge of the field. It was necessary to do this to make an assessment of the progress of plant succession based on the plant community on the adjacent uncultivated ground. The cultivated macroplot was labeled C and the uncultivated macroplot was labeled D. On both fields, each macroplot was subdivided into twenty 5- by 5-m (25 m^2) microplots marked by a grid of strings. Each macroplot was permanently marked at the corners with short lengths of half inch steel rod. Each microplot was visually searched for the presence of plant species in May 2000 when most vascular plants were in flower. The most conspicuous perennial species were counted. The number of clumps of needle-and-thread grass (*Hesperostipa comata*) and bluebunch wheatgrass in each microplot were too numerous and cumbersome to count on macroplot D on the upper field. A single microplot was randomly selected for counting. This value was used to estimate the total number of grass clumps on the entire macroplot. Sandberg's bluegrass (*Poa secunda*) was not counted because of its small stature and indiscrete clumps compared to the larger perennial grasses.

Results

Lower field

Twenty-two species were recorded at the lower field (Table 1). Of these, 16 were natives and six were alien species. Nine species occurred in 90

TABLE 1. Frequency distribution (%) and density per 500 m^2 of plant species recorded on two adjacent study plots in an abandoned field at 323 m elevation in May 2000. + = Species present in the plot, but density not counted.

	Macroplot A		Macroplot B	
	Frequency	Density	Frequency	Density
Perennials		**Native Species**		
Lupinus sulphureus	100	1205	100	1067
Crepis atrabarba	100	211	100	326
Elymus elymoides	100	200	100	358
Poa secunda	100	+	100	+
Lomatium grayi	55	20	40	10
Lomatium macrocarpum	30	17	15	6
Stipa thurberiana	25	10	15	3
Lomatium triternatum	15	5	5	2
Pseudoroegneria spicata	15	11	5	2
Agoseris grandiflora	5	1	10	3
Ericameria nauseosa	5	2	5	1
Phlox longifolia	+	+	25	23
Achillea millefolium	+	+	5	7
Erigeron filifolius	+	+	5	8
Annuals				
Draba verna	100	+	100	+
Amsinckia spp.	77	+	45	+
Perennials		**Alien Species**		
Poa bulbosa	60	+	45	+
Annuals				
Bromus tectorum	100	+	100	+
Holosteum umbellatum	100	+	100	+
Sisymbrium altissimum	100	+	100	+
Tragopogon dubius	95	+	100	+
Lactuca serriola	10	+	5	+
Total Number of Species	11.9		22	
Mean species/25 m^2 ± SE	11.9 ± 0.3		11.3 ± 0.3	

percent or more of the microplots. Of these, five were natives: hawksbeard (*Crepis atrabarba*), sulphur lupine (*Lupinus sulphureus*), bottlebrush squirreltail (*Elymus elymoides*), spring draba (*Draba verna*), and Sandberg's bluegrass. Four were alien species: cheatgrass, jagged chickweed (*Holosteum umbellatum*), tumble mustard (*Sisymbrium altissimum*), and yellow salsify (*Tragopogon dubius*). Longleaf phlox (*Phlox longifolia*), yarrow (*Achillea millefolium*), and threadleaf fleabane (*Erigeron filifolius*) were found only on macroplot B (Table 1). The mean number of species per microplot were similar on macroplots A and B (Table 1). Of the native species, Sandberg's bluegrass, sulphur lupine, hawksbeard, and bottlebrush squirreltail had the highest frequency of occurrence and were the most abundant perennial native species on the macroplots.

Upper Field

Twenty three species were found on macroplot C (Table 2). Here the vegetation was visually dominated by one-meter-tall culms of cereal rye (*Secale cereale*). The mean number of species per microplot

TABLE 2. Frequency distribution (%) and density per 500 m^2 of plant species recorded on two adjacent study plots in an abandoned field at 533 m elevation in May 2000. + = Species present in the plot, but density not counted. ( ) = estimated values.

	Macroplot C		Macroplot D	
	%Freq	Density	%Freq	Density
Perennials		**Native Species**		
Erigeron filifolius	5	8	100	376
Crepis atrabarba	5	6	100	220
Lupinus sulphureus	100	161	100	149
Pseudoroegneria spicata	30	15	100	(1120)
Hesperostipa comata	65	494	100	(1060)
Poa secunda	35	+	100	+
Achillea millefolium	15	7	95	132
Chrysothamnus viscidiflorus	5	1	80	37
Astragalus spaldingii	5	3	85	102
Calochortus macrocarpus	15	3	75	37
Lomatium triternatum	20	6	70	103
Antennaria dimorpha	0	+	55	71
Stipa thurberiana	0	+	20	4
Agoseris grandiflora	30	11	20	+
Phlox longifolia	0	+	10	6
Maceranthera canescens	0	+	10	2
Ericameria nauseosa	0	+	5	1
Annuals				
Draba verna	40	+	100	+
Epilobium paniculatum	55	+	80	+
Festuca microstachys	0	+	50	+
Lagophylla ramosissima	5	+	30	+
Amsinckia spp.	10	+	10	+
Plectriris macrocera	0	+	5	+
Perennials		**Alien Species**		
Poa bulbosa	60	+	0	+
Annuals				
Bromus tectorum	100	+	100	+
Holosteum umbellatum	100	+	100	+
Sisymbrium altissimum	100	+	80	+
Lactuca serriola	80	+	35	+
Tragopogon dubius	40	+	35	+
Secale cereale	95	+	20	+
Total Species	23		29	
mean species/25m^2 ± SE	11.2 ± 0.7		18.0 ± 0.4	

was less on macroplot C than on macroplot D (Table 2). The number of species per microplot decreased with increasing distance from the fence on macroplot C, but there was little change with increasing distance on macroplot D (Figure 1). Sulphur lupine occurred in 100% of the microplots on the cultivated ground and was the only native species with such high frequency (Table 2). The alien perennial, bulbous bluegrass (*Poa bulbosa*), was found only in macroplot C.

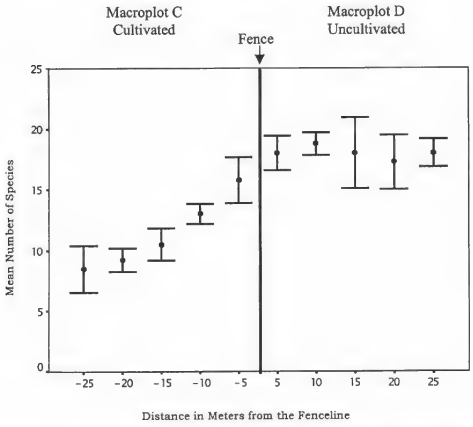

Figure 1. Mean number of species per 25 m^2 microplot and standard error (n=4 at each 5-m increment) recorded on the upper field at 5-m incremental distances on both sides of a fence.

The uncultivated macroplot D was visually dominated by clumps of native perennial bunch grasses: needle-and-thread grass, bluebunch wheatgrass, and Sandberg's bluegrass. In all, 29 species were recorded (Table 2). Thirteen species occurred in 90% or more of the microplots, of these 11 were natives: sulphur lupine, needle-and-thread grass, spring draba, Sandberg's bluegrass, bluebunch wheatgrass, hawksbeard, threadleaf fleabane, tall willowherb (*Epilobium paniculatum*), yarrow, green rabbitbrush (*Chrysothamnus viscidiflorus*), and fiddleneck tarweed (*Amsinckia* spp.). Only two were alien species: cheatgrass and jagged chickweed.

Discussion

Most of the habitat restoration work on ALE has focused on planting sagebrush shrubs in areas where it had been destroyed by recent wildfires (Durham 2000). Sagebrush provides important habitat for nesting populations of sage sparrows (*Amphispiza belli*) and loggerhead shrikes (*Lanius ludovicianus*) which are listed as species of concern by the Washington Department of Wildlife (Poole 1992, Fitzner 2000, Vander Haegen et al. 2000).

Native grasses, especially bluebunch wheatgrass, have been planted on dryland wheat fields accepted into the USDA Conservation Reserve Program in eastern Washington. However, other native species commonly associated with native stands of sagebrush and bluebunch wheatgrass habitat have seldom been used. Our data indicate that sulphur lupine, hawksbeard, Gray's lomatium (*Lomatium grayii*), nine-leaf lomatium (*L. triternatum*), bottlebrush squirreltail and Sandberg's bluegrass were the more successful native perennial species to colonize the lower field. At the upper field, the most successful species were sulphur lupine and needle-and-thread grass. Colonization by natives in the cultivated portion of the upper field may be slowed by the dominance of cereal rye, an alien species not found at the lower field. For the most part, bluebunch wheatgrass, the characteristic perennial grass of the steppe region, appears to be a poor competitor on abandoned cultivated fields even in the long-time absence of livestock grazing.

The ALE Reserve is a good place to conduct studies of plant succession because the site has a long history of freedom from livestock grazing and it is likely to be free from grazing into the future. At the present time, the major kinds of disturbances to the ALE Reserve are wildfire and grazing by a resident herd of elk (*Cervus elaphus*) (Dirkes et al. 1999). The abandoned fields provide opportunities to monitor the progress of plant succession by establishing more study plots across both fields.

Acknowledgements

The Fitzner-Eberhardt Arid Lands Ecology Reserve is owned by the United States Department of Energy and is managed by the United States Fish and Wildlife Service. Access to the Reserve is controlled. We thank the U. S. Fish and Wildlife Service, Richland, WA for permission to access the study sites. We appreciate the helpful comments provided by Dr. Lawrence Bliss and 3 anonymous reviewers on an earlier draft.

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Received 6 July 2000
Accepted for publication 21 August 2001

Northwest Science Forum

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Michael J. Wisdom, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850 Email: mwisdom@fs.fed.us

Nancy M. Warren, USDA Forest Service, Rocky Mountain Regional Office, P.O. Box 25127, Lakewood, Colorado 80225

and

Barbara C. Wales, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850

Vertebrates of Conservation Concern in the Interior Northwest: Priorities for Research

Many species of terrestrial vertebrates have been studied extensively, while others have received little research attention. In the past, the degree to which a species was studied may have depended on whether the species had commodity value (game or furbearer species, referred to as commodity species), or was threatened or endangered (listed under the U.S. Endangered Species Act, referred to as TE species). However, few studies have formally documented such patterns. In one study, broad-scale information on habitat requirements of 20 vertebrate species in Idaho was adequate for modeling the needs of most game species, but inadequate for modeling the needs of many other species of interest (Karl et al. 1999).

Within this broad group, commodity status (CS) and TE species deserve research attention. However, many species of conservation concern (species with rare or declining habitats or populations) are neither CS nor TE species, and thus may not be studied extensively. For example, birds and mammals receive more attention than amphibians and reptiles in the listing and recovery process under the U.S. Endangered Species Act, and as a result, the warm-blooded vertebrates attract more research interest (Tear et al. 1995). This presents a quandary for conservation planning: managers may know which species deserve conservation focus, but knowledge of their environmental requirements and response to management may be lacking, owing to a dearth of research.

In this essay, we identify terrestrial vertebrates of conservation concern in the Interior Northwest, and present results of a literature search used to index the degree of research conducted on these species, based on their status as CS, TE, or neither CS nor TE. Our purpose in conducting the analysis was to document research priorities of the past, and in the process, provide insight about species of conservation concern that have been under-studied and deserve increased attention in future studies.

Identifying Species of Conservation Concern

We identified terrestrial vertebrates of conservation concern from two comprehensive landscape studies (Lehmkuhl et al. 1997, Wisdom et al. 2000) conducted recently on such species in the Interior Columbia Basin and adjacent portions of the Klamath and northern Great Basins in the Interior Northwest (referred to as Basin). The Basin includes all areas drained by the Columbia River east of the Cascade Mountains in Washington, Oregon, Idaho, Montana, and Wyoming; the Klamath and Great Basins in Oregon; and small portions of the northern Great Basin in Nevada and Utah (see Figure 1, Wisdom et al. 2002). The 58 million-ha Basin encompasses a vast area of the Interior Northwest, and thus provides an opportunity to identify a comprehensive suite of species of conservation concern across a major region of the western United States.

We specifically identified 218 species from Lehmkuhl et al. (1997) and Wisdom et al. (2000) as a comprehensive suite of terrestrial vertebrates whose habitats or populations are rare or declining in the Basin (Appendix). This list included all species identified by Wisdom et al. (2000), and all but 11 species identified by Lehmkuhl et al. (1997). We dropped these 11 species because further review indicated that ranges of these species have little or no overlap with the Basin.

Identifying the 218 species as a comprehensive set of species of conservation concern appeared most appropriate because Lehmkuhl et al. (1997) and Wisdom et al. (2000) used diverse criteria to identify all potential species with rare or declining populations or habitats. That is, a variety of evidence was used to identify such species, even when available empirical data were limited but suggested a high probability of rarity or decline. Consequently, the list of 218 is likely to include most or all terrestrial vertebrates with rare or declining habitats or populations in the Basin. Not all species identified under selection criteria necessarily have rare or declining habitats or populations, only that the available evidence suggested a high probability of rarity or decline (Lehmkuhl et al. 1997, Widsom et al. 2000).

The list of 218 species was composed of 10 amphibians, 151 birds, 42 mammals, and 15 reptiles (Appendix). Birds made up the highest percentage (69%) of species, followed by mammals (19%), reptiles (7%), and amphibians (5%). These percentages were similar to the percentages of species in each vertebrate class in the Basin that were not of conservation concern. That is, of the 329 species of terrestrial vertebrates in the Basin

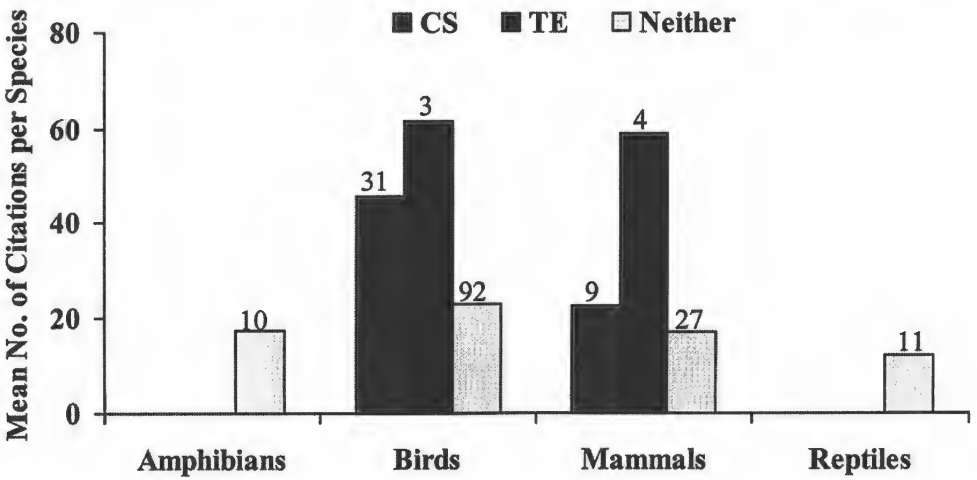

Figure 1. Mean citations per species in each management category and vertebrate class for 187 species of conservation concern identified for the Interior Columbia Basin and adjacent portions of the Klamath Basin and northern Great Basin in the western United States. Numbers of species in each management category and vertebrate class are shown above each bar.

not identified as being of conservation concern, birds composed the highest percentage (64%), followed by mammals (27%), amphibians (5%), and reptiles (4%) (Marcot et al. 1997).

Assessing Research Priorities

Our ultimate goal was to understand the implications of different categories of management on the degree to which studies have been conducted on the species of conservation concern. Consequently, we analyzed 187 of the 218 species (Appendix) in two steps: (1) by assigning each species to a unique management category that reflected special management status versus no special management status; (2) by conducting a literature search on each species and summarizing the results by management category and vertebrate class.

The 187 species included those initially selected by Wisdom et al. (2000), based on results from Lehmkuhl et al. (1997) and peer review. These 187 species were considered by Wisdom et al. (2001) to have a substantially higher probability of rare or declining habitats or populations, compared to the larger set of 218 species. Consequently, these 187 species appeared most suitable for our assessment of research priorities. The criteria used to establish and refine this list were based on Wisdom et al. (2000).

We assigned each of the 187 species to one of three management categories: (1) CS, (2) TE, or (3) neither CS nor TE (Appendix). CS species were defined as game or furbearer species harvested under requirement of hunting or trapping license by state agencies. TE species were designated as threatened or endangered under the U.S. Endangered Species Act (ESA). All other species were characterized as being neither CS nor TE species.

In a few cases, the management category of a species had changed over time. In these cases, we placed species in the category in which they were historically managed during the latter part of the 20th Century, corresponding to the time period over which most research was conducted and published. An example is Canada lynx (*Lynx canadensis*), listed in 2000 as federally threatened in the continental United States but historically managed as a furbearer. Consequently, we assigned lynx to the CS category because most research was conducted while the species had commodity status. Moreover, lynx remains a CS species outside the continental United States, where most research on the species has occurred. Another example is peregrine falcon (*Falco peregrinus*), a species historically listed as threatened but recently delisted under ESA. Consequently, we assigned peregrine falcon to the TE category (Appendix).

Admittedly, our system of categorizing species could have been refined with more categories, such as proposed or candidate species under ESA, or state-level designations of sensitive, threatened, or endangered. We explored the use of an increased number of categories, but this resulted in small sample sizes per category, with some categories containing as few as one species. These extremely low sample sizes, and highly variable sample sizes across categories, did not appear sufficient to obtain robust indices of the degree to which studies have been conducted on species in each category.

We searched for literature on the 187 species during 1997 at the University of Montana, Missoula, using all databases available at its library. We used a variety of key words to ensure that we found literature related to habitat and population status and trends, potential limiting factors, and environmental requirements. Our search was not exhaustive but instead was designed to find literature pertinent to conservation and management of each species. Our search included literature from research conducted both within and outside the Basin.

We summarized results of the literature search in three ways: (1) by management category; (2) by vertebrate class; and (3) by all combinations of management category and vertebrate class. For each summary, we calculated the mean number of citations per species.

Research is Biased by Management Category and Vertebrate Class

Of the 187 species for which we conducted a literature search, a large majority (75%) was neither CS nor TE, with a substantially smaller percentage in CS (21%) and TE (4%) categories. By contrast, mean citations per species was highest for TE species ($\bar{x}$ = 59.9), intermediate for CS species ($\bar{x}$ = 40.3), and lowest for species that were neither CS nor TE ($\bar{x}$ = 20.3). By vertebrate class, birds had the highest mean citations per species

($\bar{x}$ = 29.2), followed by mammals ($\bar{x}$ = 22.3), amphibians ($\bar{x}$ = 17.3), and reptiles ($\bar{x}$ = 12.2).

Notably, all TE and CS species were birds or mammals (Figure 1). By contrast, reptile and amphibian species, all of which lacked special status, had the two lowest mean citations (Figure 1).

These results confirm that the majority of vertebrates of conservation concern in the Interior Northwest have received little attention from research compared to those with CS or TE designations. This pattern was particularly evident for amphibians, mammals, and reptiles that were neither CS nor TE species. These vertebrates averaged <17 citations per species, lowest among all combinations of management category and vertebrate class (Figure 1). By contrast, mean citations per species for TE birds (61) and mammals (59) represented a three- to four-fold difference over species that were neither CS nor TE. Further disparities were evident from results for CS species of birds and mammals: mean citations per species for these vertebrates was 45 and 23, a level intermediate to the extremes of TE species versus those without CS or TE status.

Interestingly, a bias favoring research on birds was evident when TE species were not considered. CS birds had the highest mean citations per species among all combinations of management category and vertebrate class except TE birds and mammals (Figure 1). Moreover, mean citations per species for birds that were neither CS nor TE were equivalent to that for CS mammals, and higher than that for amphibians, mammals, and reptiles that were neither CS nor TE species.

Are New Research Priorities Needed?

Our results provide compelling evidence that research on species with special management status is heavily favored over research on species of conservation concern that lack special status. In particular, researchers have given relatively little attention to species until they become threatened or endangered, which may be a function of the availability of research funds. That is, research on a given species may not receive funding until the species is petitioned or listed as threatened or endangered. If this scenario is true, it represents a highly inefficient way to research and manage species and their habitats, in contrast to an approach that attempts to address all species of conservation concern more equitably. Without studies conducted before a species might be listed under ESA, the knowledge required to identify threats, enact appropriate conservation measures, and avoid the listing process is foregone. Clearly, a different approach is needed to address the obvious and substantial research inequities among species of conservation concern if knowledge is to be generated for efficient, preemptive management.

We believe our results could be used as a framework to develop new priorities for research on such species in the Interior Northwest. Species of conservation concern that have received little research attention in the past could be identified as having high priority for future studies. For example, lists of these species are available from a variety of private, state, and federal sources, and could be used in combination with our list to guide the development of new priorities. Species that occur consistently among such lists, and that lack special management status, would be compelling candidates for increased research emphasis.

A fundamental question about any new research priorities, in our view, is how well the new priorities mitigate past research inequities. We contend that novel designs for research on species of conservation concern must be developed by scientists and supported by managers to address past inequities. While most research has focused on single or few species (Karl et al. 1999), community-level studies are urgently needed to efficiently address the collective knowledge gaps among all species of conservation concern, especially across large landscapes such as the Basin. In an example in this issue, Wisdom et al. (2002) characterized a comprehensive network of habitats for 44 species of conservation concern in the Interior Northwest, based on estimates of habitat abundance, quality, resiliency, and connectivity derived from prior landscape research (Wisdom et al. 2000, Hann et al. 2002). Such holistic research and conservation designs are needed to deal efficiently with the large number of species that deserve conservation attention (Noss and Cooperrider 1994).

Although we advocate the development of new research priorities, we acknowledge that research on TE species is necessarily a high priority. That research, however, should not come at the expense of ignoring other species of concern whose ecological status may be just as compelling from a conservation view. Unfortunately, the listing and

recovery process under ESA is confounded by political, social, and economic considerations (Tear et al. 1995), which impede the use of this process as an ecological guide for setting research priorities. Consequently, we believe that more objective, ecological criteria are needed to develop new research priorities, in concert with use of existing processes such as those under ESA.

Professional societies in the ecological and conservation sciences are uniquely positioned to take the lead in establishing new research priorities. As independent, credible voices of science, the collective views of professional societies regarding appropriate research priorities for species of conservation concern could have substantial influence on funding decisions. For example, if a consortium of professional societies identified and published a suggested set of research priorities and designs for such species, the results could be used by a variety of private, local, state, and federal entities that fund research. While professional societies cannot make policy decisions about research funding, they can provide a clinical, diagnostic basis for others to make such decisions.

We welcome the views of scientists and managers on this topic. It is our hope that such discussion can serve as a catalyst for the design and support of more equitable ways to study all species of conservation concern in the Interior Northwest.

Acknowledgements

Tom Mills, Tom Quigley, Becky Gravenmier, and Russ Graham provided leadership and administrative support for our analysis. The Pacific Northwest Research Station and other funding sources from the USDA Forest Service and USDI Bureau of Land Management supported this work. We thank Evelyn Bull and Mary Rowland for helpful reviews of our essay, and Kevin Lair for conducting much of the literature search on which our essay is based.

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Appendix

Common and scientific names of 218 terrestrial vertebrate species of conservation concern that were identified from Lehmkuhl et al. (1997) or Wisdom et al. (2000) in the Interior Columbia Basin and adjacent portions of the Klamath and Northern Great Basins. Species of concern are those for which empirical evidence suggests rare or declining habitats or populations. Species are placed in categories of CS (commodity: game or furbearer species), TE (threatened or endangered under U.S. Endangered Species Act), or neither CS nor TE.

TE (Threatened or Endangered)[1]	
Bald eagle	*Haliaeetus leucocephalus*
Western snowy plover	*Charadrius alexandrinus nivosus*
Whooping crane	*Grus americana*
Gray wolf	*Canis lupus*
Grizzly bear	*Ursus arctos*
Idaho ground squirrel	*Spermophilus brunneus*
Woodland caribou	*Rangifer tarandus caribou*
Peregrine falcon[2]*	*Falco peregrinus*
CS (Commodity)	
American wigeon	*Anas americana*
Band-tailed pigeon	*Columba fasciata*
Barrow's goldeneye	*Bucephala islandica*
Blue grouse	*Dendragapus obscurus*
Blue-winged teal	*Anas discors*
Bufflehead	*Bucephala albeola*
Canvasback	*Aythya valisineria*
Cinnamon teal	*Anas cyanoptera*
Columbian sharp-tailed grouse	*Tympanuchus phasianellus colombianus*
Common goldeneye	*Bucephala clangula*
Common merganser	*Mergus merganser*
Common snipe	*Gallinago gallinago*
Gadwall	*Anas strepera*
Greater sage-grouse	*Centrocercus urophasianus*
Greater sandhill crane	*Grus canadensis tabida*
Green-winged teal	*Anas crecca*
Harlequin duck	*Histrionicus histrionicus*
Hooded merganser	*Lophodytes cucullatus*
Lesser scaup	*Aythya affinis*
Mallard	*Anas platyrhynchos*
Mountain quail	*Oreortyx pictus*
Northern pintail	*Anas acuta*
Northern shoveler	*Anas clypeata*
Redhead	*Aythya americana*
Ring-necked duck	*Aythya collaris*
Ruddy duck	*Oxyura jamaicensis*
Sora	*Porzana carolina*
Trumpeter swan	*Cygnus buccinator*
Virginia rail	*Rallus limicola*
Wood duck	*Aix sponsa*
Yellow rail	*Coturnicops noveboracensis*
American marten	*Martes americana*
California bighorn sheep	*Ovis canadensis californiana*
Fisher	*Martes pennanti*
Lynx	*Lynx canadensis*
Mountain goat	*Oreamnos americanus*
Pronghorn	*Antilocapra americana*
Rocky mountain bighorn sheep	*Ovis canadensis*
Western gray squirrel	*Sciurus griseus*
White-tailed jackrabbit*	*Lepus townsendii*
Wolverine	*Gulo gulo*
Neither CS nor TE	
Coeur D'alene salamander	*Plethodon idahoensis*
Columbian spotted frog	*Rana luteiventris*
Idaho giant salamander	*Dicamptodon aterrimus*
Larch mountain salamander	*Plethodon larselli*
Northern leopard frog	*Rana pipiens*
Oregon spotted frog	*Rana pretiosa*
Tailed frog	*Ascaphus truei*
Western toad	*Bufo boreas*
Wood frog	*Rana sylvatica*
Woodhouse's toad	*Bufo woodhousii*
American avocet	*Recurvirostra americana*
American bittern	*Botaurus lentiginosus*
American redstart	*Setophaga ruticilla*
American white pelican	*Pelecanus erythrorhynchos*
Ash-throated flycatcher	*Myiarchus cinerascens*
Baird's sandpiper	*Calidris bairdii*
Barred owl	*Strix varia*
Black rosy-finch	*Leucosticte atrata*
Black tern	*Chlidonias niger*
Black-backed woodpecker	*Picoides arcticus*
Black-bellied plover	*Pluvialis squatarola*
Black-chinned hummingbird	*Archilochus alexandri*
Black-crowned night heron	*Nycticorax nycticorax*
Black-necked stilt	*Himantopus mexicanus*
Black-throated sparrow	*Amphispiza bilineata*
Bobolink	*Dolichonyx oryzivorus*
Boreal owl	*Aegolius funereus*
Brewer's blackbird	*Euphagus cyanocephalus*

* Species for which no literature search was completed

[1] Threatened or Endangered under U.S. Endangered Species Act

[2] Peregrine falcon is not currently designated as TE but was historically designated as such.

[3] Brown-headed cowbird is not rare or declining, but was identified as a species of concern because of its spread throughout the Basin during the past century and subsequent negative effects, via brood parasitism, on a variety of bird species

Brewer's sparrow	*Spizella breweri*
Broad-tailed hummingbird	*Selasphorus platycercus*
Brown creeper	*Certhia americana*
Brown-headed cowbird[3]	*Molothrus ater*
Burrowing owl	*Athene cunicularia*
Bushtit	*Psaltriparus minimus*
California gull	*Larus californicus*
Caspian tern*	*Sterna caspia*
Chestnut-backed chickadee	*Poecile rufescens*
Chipping sparrow*	*Spizella passerina*
Clark's grebe	*Aechmophorus clarkii*
Clay-colored sparrow	*Spizella pallida*
Common loon	*Gavia immer*
Cooper's hawk*	*Accipiter cooperii*
Downy woodpecker	*Picoides pubescens*
Dunlin*	*Calidris alpina*
Ferruginous hawk	*Buteo regalis*
Flammulated owl	*Otus flammeolus*
Forster's tern	*Sterna forsteri*
Fox sparrow	*Passerella iliaca*
Golden-crowned kinglet	*Regulus satrapa*
Grasshopper sparrow	*Ammodramus savannarum*
Gray-crowned rosy finch	*Leucosticte tephrocotis*
Great blue heron	*Ardea herodias*
Great egret	*Ardea alba*
Great gray owl	*Strix nebulosa*
Greater yellowlegs*	*Tringa melanoleuca*
Green-tailed towhee*	*Pipilo chlorurus*
Hairy woodpecker*	*Picoides villosus*
Hammond's flycatcher	*Empidonax hammondii*
Hermit warbler	*Dendroica occidentalis*
Horned lark*	*Eremophila alpestris*
Lark bunting	*Calamospiza melanocorys*
Lark sparrow	*Chondestes grammacus*
Lazuli bunting	*Passerina amoena*
Least flycatcher	*Empidonax minimus*
Least sandpiper*	*Calidris minutilla*
Lesser yellowlegs*	*Tringa flavipes*
Lewis' woodpecker	*Melanerpes lewis*
Loggerhead shrike	*Lanius ludovicianus*
Long-billed curlew	*Numenius americanus*
Long-billed dowitcher*	*Limnodromus scolopaceus*
Long-eared owl	*Asio otus*
Marbled godwit*	*Limosa fedoa*
Merlin	*Falco columbarius*
Northern goshawk	*Accipiter gentilis*
Northern pygmy-owl*	*Glaucidium gnoma*
Northern saw-whet owl*	*Aegolius acadicus*
Olive-sided flycatcher	*Contopus cooperi*
Pectoral sandpiper*	*Calidris melanotos*
Pileated woodpecker	*Dryocopus pileatus*
Pine siskin	*Carduelis pinus*
Pygmy nuthatch	*Sitta pygmaea*
Red-eyed vireo	*Vireo olivaceus*
Red-naped sapsucker	*Sphyrapicus nuchalis*
Red-necked grebe	*Podiceps grisegena*
Red-necked phalarope*	*Phalaropus lobatus*
Red-winged blackbird*	*Agelaius phoeniceus*
Ring-billed gull	*Larus delawarensis*
Rufous hummingbird	*Selasphorus rufus*
Rufous-sided towhee*	*Pipilo erythrophthalmus*
Sage sparrow	*Amphispiza belli*
Sage thrasher	*Oreoscoptes montanus*
Sanderling*	*Calidris alba*
Semipalmated plover*	*Charadrius semipalmatus*
Semipalmated sandpiper*	*Calidris pusilla*
Short-eared owl	*Asio flammeus*
Snowy egret	*Egretta thula*
Spotted sandpiper	*Actitis macularia*
Swainson's hawk*	*Buteo swainsoni*
Three-toed woodpecker	*Picoides tridactylus*
Tricolored blackbird	*Agelaius tricolor*
Upland sandpiper	*Bartramia longicauda*
Varied thrush	*Ixoreus naevius*
Vaux's swift	*Chaetura vauxi*
Veery	*Catharus fuscescens*
Vesper sparrow	*Pooecetes gramineus*
Virginia warbler	*Vermivora virginiae*
Western bluebird	*Sialia mexicana*
Western grebe	*Aechmophorus occidentalis*
Western least bittern	*Ixobrychus exilis hesperis*
Western meadowlark	*Sturnella neglecta*
Western sandpiper*	*Calidris mauri*
Western screech-owl	*Otus kennicottii*
Western tanager*	*Sitta carolinensis*
White-faced ibis	*Plegadis chihi*
White-headed woodpecker	*Picoides abolarvatus*
White-winged crossbill	*Loxia leucoptera*
Willet	*Catoptrophorus semipalmatus*
Williamson's sapsucker	*Sphyrapicus thyroideus*
Willow flycatcher	*Empidonax traillii*
Wilson's phalarope	*Phalaropus tricolor*
Wilson's warbler	*Wilsonia pusilla*
Winter wren	*Troglodytes troglodytes*
Yellow warbler	*Dendroica petechia*
Yellow-billed cuckoo	*Coccyzus americanus*
Yellow-breasted chat	*Icteria virens*
Cliff chipmunk	*Tamias dorsalis*
Fringed myotis	*Myotis thysanodes*
Hoary bat	*Lasiurus cinereus*
Kit fox	*Vulpes macrotis*
Long-eared myotis	*Myotis evotis*
Long-legged myotis	*Myotis volans*
Northern bog lemming	*Synaptomys borealis*
Northern flying squirrel	*Glaucomys sabrinus*
Pallid bat*	*Antrozous pallidus*
Pinyon mouse	*Peromyscus truei*
Potholes meadow vole	*Microtus pennsylvanicus kincaidi*
Preble's shrew	*Sorex preblei*
Pygmy rabbit	*Brachylagus idahoensis*
Pygmy shrew	*Sorex hoyi*
Sagebrush vole	*Lemmiscus curtatus*
Silver-haired bat	*Lasionycteris noctivagans*
Spotted bat	*Euderma maculatum*

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Uinta chipmunk	*Tamias umbrinus*	Ground snake	*Sonora semiannulata*
Uinta ground squirrel	*Spermophilus armatus*	Longnose leopard lizard	*Gambelia wislizenii*
Washington ground squirrel	*Spermophilus washingtoni*	Longnose snake	*Rhinocheilus lecontei*
Water shrew	*Sorex palustris*	Mojave black-collared lizard	*Crotaphytus bicinctores*
Water vole	*Microtus richardsoni*		
Western small-footed myotis	*Myotis ciliolabrum*	Night snake*	*Hypsiglena torquata*
White salmon pocket gopher	*Thomomys talpoides limosus*	Painted turtle	*Chrysemys picta*
White-tailed antelope squirrel	*Ammospermophilus leucurus*	Rubber boa	*Charina bottae*
Wyoming ground squirrel	*Spermophilus elegans*	Sagebrush lizard*	*Sceloporus graciosus graciosus*
Yuma myotis	*Myotis yumanensis*	Sharptail snake	*Contia tenuis*
California mountain kingsnake	*Lampropeltis zonata*	Short-horned lizard*	*Phrynosoma douglassii*
		Striped whipsnake	*Masticophis taeniatus*
Common garter snake	*Thamnophis sirtalis*	Western pond turtle	*Clemmys marmorata*

Northwest Science Forum

David L. Wilderman, Washington Department of Natural Resources, 713 Bowers Road, Ellensburg, Washington, 98926

Botanical Research Opportunities in the Columbia River Gorge, Washington

The Columbia River Gorge exhibits dramatic environmental and geographic gradients, and as a result, contains truly distinctive vegetation patterns. These patterns are aptly described in this issue (Wolter and Fonda 2002). Within the Gorge, a wide variety of habitats are in relatively close proximity to each other, and the region supports some species assemblages not found in other portions of Washington. In addition, the area is well-known for its unique flora, which includes 15 plant taxa endemic to the Gorge and immediate surroundings (Jolley 1988). Despite these intriguing biological characteristics, however, the Columbia River Gorge has received relatively sparse attention with regard to recent research. I would like to encourage readers to consider the many opportunities for research in the Gorge by highlighting some of the publicly-owned sites that have been protected specifically for research and education, and by pointing out some of the research questions relevant to the area.

As an ecologist with the Washington Department of Natural Resources (DNR) Natural Areas Program, I help monitor and manage Natural Area Preserves (NAPs) and Natural Resource Conservation Areas (NRCAs) in Washington State. These lands are managed by DNR specifically for research, education, and in the case of NRCAs, low-impact recreation. The sites are selected and established based on the presence of relatively undisturbed examples of plant communities that can serve as research baselines and/or the presence of significant populations of rare plant or animal taxa.

In the Columbia River Gorge and vicinity, there are five (soon to be six) NAPs and three NRCAs. These sites are distributed from the western end to the eastern end of the Gorge, and they support examples of the potential natural vegetation in each of the physiognomic plant associations described by Wolter and Fonda (2002). This includes old-growth Douglas-fir-western hemlock (*Pseudotsuga menziesii-Tsuga heterophylla*) forest at the western end of the Gorge, Douglas-fir/Oregon white oak (*Quercus garryana*) forest and Oregon white oak-ponderosa pine (*Pinus ponderosa*) woodland in the middle Gorge, and bluebunch wheatgrass-Idaho fescue (*Agropyron spicatum-Festuca idahoensis*) steppe in the eastern Gorge. In addition to these physiognomic groupings, other associations and habitats, such as wetlands, riparian forest, balds, and lithosolic shrub-steppe communities, are represented. The sites also support populations of nine of the 15 plant taxa endemic to the Gorge, and populations of other rare plant and animal taxa.

The Gorge environment and biota have the potential for a variety of interesting research topics. Studies examining the fire history and fire ecology of the area would provide important information to land managers, especially those trying to manage for natural conditions, to help determine appropriate management strategies. Invasive non-native plant species are a threat to native species and communities throughout the Gorge, and more knowledge is needed regarding the effectiveness of various control methods. Efforts to manage for rare species require detailed information on the ecology of particular habitats and populations, particularly where experimental habitat manipulation is being considered. For most of the rare plant taxa in the Gorge, only a limited amount of such information is available.

A number of more basic research questions are unique to the Columbia River Gorge. The biogeography of the area is of particular interest,

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as the Gorge has served as a major east-west migration route through the Cascades for plants and animals (Detling 1961, 1966, 1968). In fact, the Gorge is the only near sea-level route through the Cascades between the Fraser River to the north and the Klamath River to the south (Detling 1966). The mixing of eastside and westside plant taxa is exemplified by the distributions of Puget balsamroot (*Balsamorhiza deltoidea*) and Roemer's fescue (*Festuca roemeri*), species that are otherwise restricted to the Puget Trough and Willamette Valley, but are found well to the east in the Columbia River Gorge. The point at which these species give way to Carey's balsamroot (*Balsamorhiza careyana*) and Idaho fescue (*Festuca idahoensis*), the congeneric species more typical of eastern climes, and the degree to which they intermingle, are examples of research questions of interest. Another example is the need to determine the taxonomic relationship of obscure buttercup (*Ranunculus reconditus*), one of the taxa considered endemic to the Gorge, to a similar species found in Nevada and Idaho.

These are but a few examples of the types of interesting and useful research that could be conducted in the Columbia River Gorge. Undoubtedly other scientists could add substantially to the list. My hope is that by shedding some light on a few of the research needs and opportunities in the Gorge, as well as the value of the Natural Area Preserves and Natural Resource Conservation Areas in the area for research, more interest will be generated and researchers will become more active in the area. For more information on NAPs and NRCAs, including those in the Columbia River Gorge, visit the DNR home page at www.wa.gov/dnr.

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Book Review

Year of the Fires: The Story of the Great Fires of 1910

Stephen J. Pyne, 2001, Viking Press, New York, 322 Pages. ISBN 0-670-89990-9. Hardcover, $25.95

The tragic fatalities of four firefighters in 2001 on the Thirtymile Fire on the Okanogan National Forest remind us that fire suppression is a dangerous business. As with the 1994 firefighter fatalities on Storm King Mountain in Colorado, firefighting tragedies may have policy as well as tactical implications. But neither 1994 nor 2001 will be remembered as the Year of the Great Fires. That date is reserved for 1910, when 3.25 million acres burned and 88 firefighters died in the northern Rocky Mountains. These Idaho and Montana fires were not larger than those before or since, and killed far fewer people than earlier fires in Michigan and Minnesota, but had a massive policy impact because of their cultural context. They occurred just as the Progressive movement was championing conservation, and had the effect of cementing a fire exclusion policy on America's landscape for the better part of the twentieth century. Washingtonians and Oregonians will remember from their history books that 1902 was a much worse regional fire year. Yet the policy impact of the 1910 fires were as different from those of 1902 as Rocky Mountain oysters are from their Olympia cousins. Stephen Pyne does a masterful job of telling this story in the context of its time, history at its best.

Year of the Fires is organized as a chronological narrative of 1910, with chapters from January to December. In the below-normal snowpack months of January to April, Pyne's focus is on the political climate in Washington, D.C., interspersed with personal histories of those who would become prominent in the summer wildfire battles. President Taft had just fired Gifford Pinchot, the fiery chief of the five-year-old Forest Service, and Pinchot's Progressive forestry agenda that prominently featured elimination of free-burning fire was at risk. Debates of the merits of "light burning" forests where fire was once frequent were at a peak, with popular articles in *Sunset Magazine* advocating use of light fires. The fires of 1910 doused the debate, even though it smoldered for another decade. While local forest rangers in Idaho and Montana interpreted the fires as a major defeat, the political context in Washington, D.C. was that victory was in sight. This was the time when the fledgling Forest Service "...drew a line in the duff." The 1910 fires were used to reinforce the need for a national fire exclusion policy and the resources necessary to implement it, and Congress followed that lead. Pyne shows that while the Forest Service lost the fight in the woods, it won the greater war for the public mind.

The chapters of July and August fill about a quarter of the book, swelling the narrative, in Pyne's words, to demonstrate the surge of the fires. He weaves an exciting, dangerous tale of a parched forest landscape with myriad fires ebbing and flowing in July and early August. Just when the firefighters thought the situation was under control, another weather event would blow the fires out of control again. The efforts of hardworking logging gangs and Army troops, supplemented by ragtag bands of men plucked from saloons and flophouses and led by a few dedicated rangers who had little experience with fire, makes one wonder that only 88 fatalities were recorded. Most died during the "Big Blowup" on August 20-21; all were firefighters, and were there by choice, although few understood that choice. Major firestorms blown by strong winds crackled over the Idaho-Montana border area, blowing fires into the crowns of trees over hundreds of square miles simultaneously, trapping firefighters, burning towns, with the power to uproot whole stands of cedar and white pine. The smoke and soot from the Big Blowup reached as far as Greenland. Pyne jumps from heroic episode to tragic circumstance, just as the fires jumped from tree to tree, in a narrative form that clearly conveys the chaos of the moment.

Stories of heroism and sacrifice abound, but none resonates as much as that of Ed Pulaski. Pulaski was a ranger caught in the Big Blowup who led 44 men (and two horses) into a mine shaft and stood guard at the entrance, beating out flames

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and with pistol in hand, threatening to shoot anyone who tried to leave. All but five men and the two horses survived, although most survivors were rendered unconscious by the heat and smoke. Pyne tells the story with all of its ambiguities, as Pulaski was notably reluctant to tell his own story. Pulaski's legacy is as a man who acted courageously in extraordinary circumstances, and who developed the axe-mattock tool that bears his name and became a standard firefighting tool.

Pyne notes that the 1910 conflagrations were spliced into the Forest Service institutional genes, shaping the Forest Service as profoundly by the Great Fires as modern China by the Long March. He brings that year to life like no other story of those fires, in an engaging narrative that you will find hard to put down. Anyone wishing to participate in current wildland fire policy debates needs to have read this book as mandatory background material. Stephen Pyne has crafted a masterful narrative of the fires and their cultural impact. He weaves in Clementsian ecological theory, Progressivism, and William James' pragmatic philosophy. Ironically, James's argument to conscript young people to fight against nature, "The Moral Equivalent of War", was published in *McClure's Magazine* the month of the Big Blowup. Pyne has been generally considered to be the world's foremost authority on fire and its role in human culture. After reading this book, I conclude that we simply should acknowledge that he *is* the foremost authority.

—James K. Agee
College of Forest Resources
University of Washington
Seattle, WA 98195

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Volume 75 (2001)
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NORTHWEST SCIENCE

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Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

Theses, dissertations, and articles in press

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Revised February 2002

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WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Presorted Standard
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*

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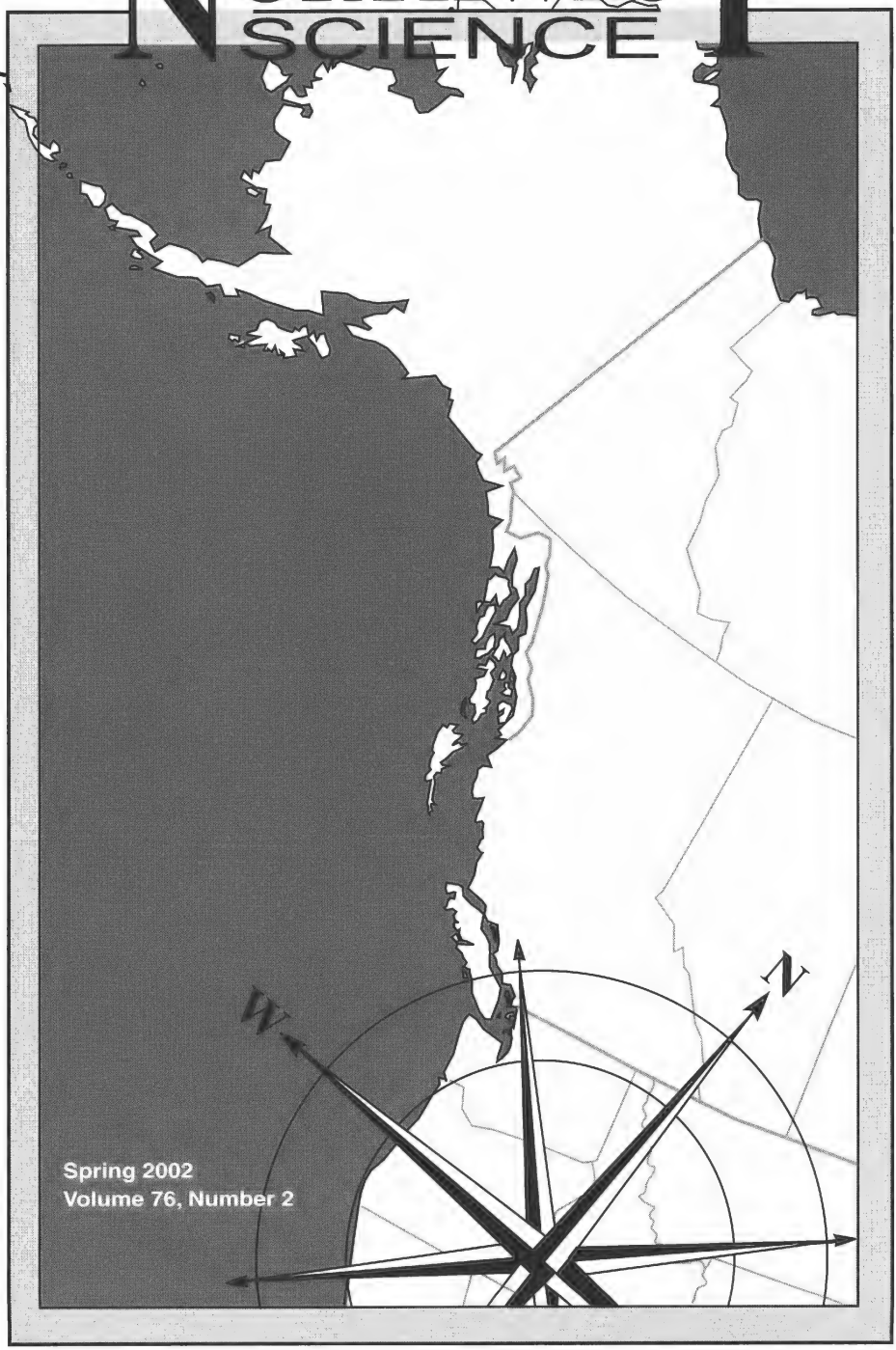

Spring 2002
Volume 76, Number 2

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Editor of *Northwest Science*

Rich Fonda
Biology Department
Western Washington University
Bellingham, Washington 98225
Telephone: 360-650-6599
Fax: 360-650-3148
Internet: fonda@biol.wwu.edu

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Randall C. Morris
Environmental Science and Research Fndn.
101 S. Park Ave./PO Box 51838
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Information for Authors

Announcements

2002 Student Research Grant Awards

Each year the Northwest Scientific Association awards grants to several students who have submitted outstanding research proposals. Congratulations to this year's research grant winners, who were announced at the 2002 NWSA meeting in Boise, Idaho:

- Melissa Borsting, University of Washington, "Effects of thinning and prescribed fire on understory vegetation in ponderosa pine forests"
- John Citta, University of Montana, "The role of different habitat types in the population dynamics of a fire associated cavity nesting bird, the mountain bluebird"
- Suzanne Cox, University of Montana, "Evaluation of the long-term population trends of the Olympic marmot"
- Joseph Rauch, Boise State University, "Genetic consequences of invasive plant introductions: an analysis of northwest United States *Taeniatherum caput-medusae* (medusahead) populations"

Ross Black elected President for 2002-2004

Dr. Ross Black is the new president of the Northwest Scientific Association, replacing Dr. Tim Reynolds. Our thanks go to Tim for his excellent leadership while President.

Ross, a native of the Puget Sound Basin, has been interested in aquatic environments since his youth when he moved to the shores of a small eutrophic lake in King County. Ross earned a B.S. in fisheries from the University of Washington in 1985. At the UW, he studied aquatic ecology, learned to love field work, and came to appreciate experimental ecology while spending his summers working on the Grays Harbor and Willapa Bay estuaries of the southeast Washington coast. A desire to study something new led Ross to the University of Wisconsin-Madison for M.S. and Ph.D. degrees in Zoology, where his graduate work focused on the ecology and evolution of inducible defenses in pond invertebrates. Following postdoctoral studies at the University of Louisville, Ross accepted a faculty position at Eastern Washington University. He is currently an associate professor, conducting research on the ecology of pond, reservoir, and mountain lake organisms, and teaching courses in ecology, evolution, and aquatic biology.

Craig A. Barfoot,[1] **Dena M. Gadomski,**[2] and **James H. Petersen,** U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605

Resident Fish Assemblages in Shallow Shorelines of a Columbia River Impoundment

Abstract

During May-September 1995, we replicated an earlier (1984-85) study of fishes in shoreline habitats of the John Day Reservoir, Columbia River, to investigate fish assemblage structure at several spatial and temporal scales. A total of 37,400 resident fishes representing 24 taxa was collected in 359 beach seine hauls. Fish catch composition during 1984 and 1985 was very similar, but was greatly different from catch in 1995. During 1984-1985, four native taxa (chiselmouth, northern pikeminnow, suckers, and sand rollers) constituted more than 90% of the combined main-channel catch, with introduced taxa comprising only 1.3% of the main-channel catch. In contrast, during 1995 only 37.7% of the main-channel catch comprised chiselmouth, northern pikeminnow, suckers, and sand rollers, while 33.9% were introduced taxa, primarily sunfishes and yellow perch. This shift in catch composition was greatest in the lower reservoir where the 1995 catch was 61% introduced taxa. Although changes in species composition of near-shore reservoir fish assemblages over the 10-yr period appeared to be substantial, we are unsure of annual variability since we have only one season of sampling for comparison with the earlier study. The differences we observed could be a long-term response to reservoir aging, a short-term reaction to annual differences in hydrologic and thermal regimes, or simply the naturally varying reproductive success of some species.

Introduction

Fish assemblages in the Columbia River Basin were historically dominated by salmonids and cottids, which were 39-50% and 20-30% of the fishes collected in Oregon streams and rivers from 1900 to the mid-1940s (Li et al. 1987). In the past century, however, aquatic environments have been greatly altered by land-use practices such as farming, timber harvesting, and hydroelectric development (Lichatowich 1999). In the United States portion of the Columbia River Basin for example, 11 large hydroelectric dams were constructed between 1933 and 1968 (Ebel et al. 1989), creating reservoirs where the average water velocity is lower, water temperature increases earlier in the season and remains high longer into the fall (Quinn and Adams 1996), and fine sediments have accumulated behind dams, thus changing substrate composition. Concurrent with these changes in aquatic habitats, introduced non-native warmwater and coolwater fishes, such as centrarchids and percids, have proliferated (Li et al. 1987, Poe et al. 1994).

Despite these large-scale changes in basin aquatic habitats and biotic assemblages, few multi-taxa accounts of resident fishes (non-anadromous) in main-stem impoundments exist. Li et al. (1987) and Poe et al. (1994) provide descriptive accounts of historic and recent fish assemblages, with some data on temperature preferences and trophic relationships. Gray and Dauble (1977) estimated the relative abundance of fishes in the unimpounded Hanford Reach of the Columbia River. Species lists with abundance data are available for some reservoirs in agency reports (Nigro 1988). Research in the basin has primarily focused on salmonids and white sturgeon (*Acipenser transmontanus*), with some studies on predators of juvenile salmonids such as northern pikeminnow (*Ptychocheilus oregonensis*) and smallmouth bass (*Micropterus dolomieu*).

Identifying the composition and dynamics of reservoir fish assemblages is important to fishery managers who must develop strategies for recovering endangered species, but still allow for sport, tribal, and commercial fisheries along with other competing uses of waterways in the basin. Management agencies within the Pacific Northwest are currently considering several changes to the hydrosystem and its operation (e.g., dam breaching, reservoir drawdowns, seasonal water budgeting) and to fishery management strategies (e.g., liberalized harvest of introduced taxa) in

[1]Current address: Tribal Fisheries, Confederated Salish and Kootenai Tribes, Box 278, Pablo, MT 59855

[2]Author to whom correspondence should be addressed. E-mail: dena_gadomski@usgs.gov

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an attempt to recover severely depressed salmonid populations. These proposed management actions could greatly alter the habitat and fish species composition of impounded reaches.

The objective of this study was to examine the temporal and spatial composition of shoreline fish assemblages in John Day Reservoir, the largest impoundment (123 km in length) on the lower Columbia River (Figure 1). Shorelines are important habitats for all life stages of resident fishes, often providing shelter and abundant food resources. However, shallow shoreline habitats may be particularly vulnerable to hydrosystem operations, and changes in water levels and flows that result in altered environmental conditions may subsequently cause changes in fish assemblages. We determined if changes in fish assemblage structure have occurred in John Day Reservoir, which was impounded in 1968, by examining fish composition in four main-channel locations and two backwater areas at three temporal scales: within-year (spring compared to summer), annual (1984 compared to 1985), and over a long time interval (1984-1985 compared to 1995). Changes in fish assemblages over time were additionally determined at two spatial scales. We examined the six John Day Reservoir locations individually, and also pooled sites by either main-channel or backwater area.

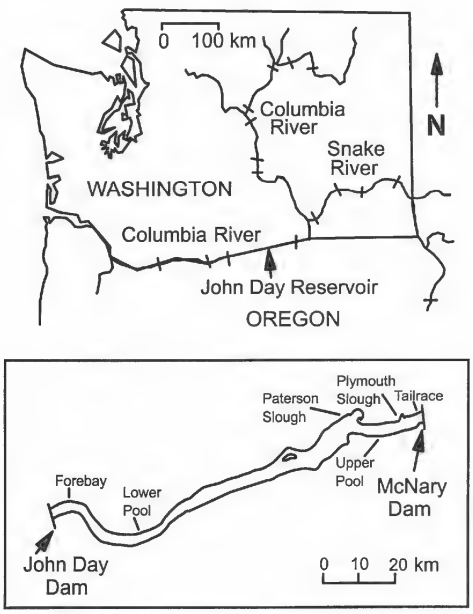


Figure 1. Beach seine sample sites in the John Day Reservoir, Columbia River. Fishes were sampled at six major locations in the reservoir.

Methods

Study Area and Field Methods

During 1995 we replicated an earlier (1984-1985) study (Gray et al. 1984, Palmer et al. 1986) of resident fish assemblages in shoreline areas of the John Day Reservoir. The upper third of the reservoir contains extensive shallow-water habitat in main-channel and backwater areas. Farther downriver, banks become steep-sided with limited shallow-littoral habitat. Substrate is mud, sand, gravel, and cobble (Parsley et al. 1993). Dominant substrates at the sample sites ranged from fine sediment to cobble. Growths of aquatic macrophytes, primarily water milfoil (*Myriophyllum* spp.), are seasonally abundant in littoral areas, particularly in shallow embayments and backwater habitats.

We sampled fishes with a beach seine at four shoreline sites at each of four main-channel locations: the tailrace, forebay, and the upper and lower pool (pool is defined as the area of the reservoir excluding the tailrace and forebay); and in two backwaters: Plymouth and Paterson sloughs (Figure 1). This typically resulted in 24 beach seine hauls per sampling period, with the four sites at each location considered a sample. In 1984 and 1985, fish samples were collected on a monthly basis from April through August (except July) at each of the six study locations. In 1995 we sampled on a biweekly schedule from May through August. During late June through August of 1995, we were unable to sample at any site in the Paterson Slough backwater location because of water milfoil abundance.

Fish samples were collected at night using 30.5 x 2.4 m beach seines with a 2.4 m^2 central bag and 6.4-mm knotless nylon mesh. Leads (15.2 m) and weighted brails were attached to both ends of the seine. To conduct a seine haul, one end of the seine was anchored to the shoreline by attaching the lead to streamside vegetation or to a metal stake driven into the ground, and the opposite lead was attached to a cleat on the bow of a

boat. The seine was deployed by backing the boat in a semicircle until water depth was insufficient for boat operation; the seine was then manually pulled to shore using the lead ropes. This method of sampling is not without biases, i.e., capture efficiency can be influenced by the habitat types being sampled, and by size- and species-specific behavioral differences. We attempted to minimize or maintain the consistency of these problems by sampling only at night, by restricting the size of the fish included in the analyses, and by sampling at the same sites across years with generally equal effort among locations within a year.

For comparison with the 1984-85 data sets (Gray et al. 1984, Palmer et al. 1986), only fish 250 mm or less in fork length were retained. These were measured to the nearest mm and identified to the lowest possible taxon. Most fishes were released after sampling, however, large catches of small fish were preserved in 10% formalin and returned to the laboratory for processing. Some suckers (*Catostomus* spp.), bullheads (*Ameiurus* spp.), sculpins (*Cottus* spp.), and sunfishes (*Lepomis* spp. and *Pomoxis* spp.) were inconsistently identified to species between the two study periods. Because of this, these fishes were grouped into their respective genera for analysis (Table 1).

To describe environmental conditions during each season, we obtained daily discharge and temperature information from StreamNet (2001).

Data Analysis

We examined the similarity of resident fish assemblages at various temporal scales by calculating Spearman's rank correlation coefficients (r_s) on the ordered abundances of the most commonly collected fish taxa. The anadromous fishes American shad (*Alosa sapidissima*) and juvenile salmonids (*Oncorhynchus* spp.) were not included in these analyses because of large temporal variations in abundance. Rank correlation analyses are commonly used to assess temporal concordance of fish assemblages (Ross et al. 1985, Bass 1990). However, the use of such analyses has been questioned because the strength of the association and the significance of the test can be influenced by including large numbers of rare species. Since all species are equally important in the analysis, small changes in the rank orders of uncommon species could outweigh relatively large changes in the ranks of more abundant species (Grossman et al. 1982). Thus, we restricted our analyses to the 10 overall most abundant taxa for the sample periods being compared. Since this restriction always retained an average abundance of at least 90% of the fishes collected, the analyses still included those taxa that were the most important in the assemblage structure (Matthews et al. 1988).

We examined seasonal, annual, and long-term continuity of assemblage structure. Seasonal continuity was assessed by comparing spring (April-May in 1984 and 1985; May in 1995) with summer (June and August in 1984 and 1985; June-August in 1995) catches to determine if temporal changes in fish habitat use or an increased abundance of young-of-the-year fishes in the summer caused large shifts in the rank orders of the most common taxa. Annual assemblage continuity was examined by comparing 1984 taxa ranks to 1985 ranks, and long-term continuity was assessed by comparing the ranks of the pooled 1984-85 catches to the 1995 taxa ranks. Seasonal and annual assemblage changes were compared at each of the six sample locations of the reservoir, while long-term changes were only examined at main-channel locations because of some backwater sample site differences in 1995. Changes in assemblage structure were also examined at larger spatial scales by comparing catches pooled across all main-channel locations of the reservoir and by comparing catches pooled across both backwater locations.

We also examined assemblage similarities using Schoener's (1968) proportional similarity index (PSI) (Meffe and Sheldon 1990). The index varies from zero to one, with a value of zero indicating no similarity. Indices are not statistical tests, but they do provide a relative assessment of assemblage similarity (Matthews et al. 1988, Meffe and Sheldon 1990). In addition, PSI values, unlike rank order analyses, may not be as sensitive to the inclusion of rare taxa in the calculations. Thus, we computed PSI values on the entire taxa list for each of the periods being compared.

We used principal components analysis (PCA) to identify fish taxa associations and to assess assemblage composition in time and space (Rose and Echelle 1981, Moyle et al. 1986, Finger and Stewart 1987, Ross et al. 1987, Meng et al. 1994, Mahon et al. 1998, Hoff and Bronte 1999). The PCA was conducted on a correlation matrix of the 10 overall most abundant taxa; these made

up an average of ≈97% of the reservoir-wide annual catch and excluded those taxa that generally made up < 1% of the total annual catch. We first averaged the individual seine haul data by month for each of the six locations. Input data were the arcsine-square root transformed proportions of each taxon for each year-month-location combination (3 yr x 4 mo x 6 locations). Samples were not available for the forebay and lower pool locations during April 1984, or for the Paterson Slough location during July and August 1995; thus, the PCA was conducted on 68 monthly samples. Fish taxa associations were identified by plotting taxa loadings on the first and second principal components (PC) (Carpenter et al. 1981). We then graphically examined temporal and spatial relations of catches at the sample locations by plotting the scores of each year-month-location combination on the first two principal components (Finger and Stewart 1987, Ross et al. 1987).

Results

Overview of Resident Fish Catch

During the 3 yrs of sampling (1984, 1985, 1995), 37,400 resident fishes representing 9 families and 24 taxa were collected in 359 seine hauls. Although young age classes were important in the catch, length frequency information for the 10 overall (pooled across years and locations) most abundant taxa indicated that most species were represented by two or more year classes. The exception to this was smallmouth bass, which were almost all age-0 individuals (Figure 2). Of the 24 resident fish taxa collected, 13 species were introduced (Table 1). The same taxa were collected in all years, except goldfish (*Carassius auratus*) was absent in 1985, and speckled dace (*Rhinichthys osculus*), an uncommon species in 1984-1985, was not collected in 1995.

Native fishes dominated the combined main-channel catches in all 3 yrs, but to a much lesser extent in 1995 (Table 2). In the earlier sampling period (1984-1985) four native taxa (chiselmouth, northern pikeminnow, suckers, and sand rollers) constituted more than 90% of the combined main-channel catch, with introduced taxa comprising only 1.3% of the catch. In contrast, during 1995 only 37.7% of the main-channel catch comprised chiselmouth, northern pikeminnow, suckers, and sand rollers, while introduced taxa made up 33.9% of the catch. The greater percentage of introduced fish in the 1995 catch was primarily due to an increase in the relative abundance of sunfishes and yellow perch. In pooled backwater catches, the percentage of introduced fishes remained similar between the earlier sampling period (28.4%) and 1995 (33.6%). The dominant introduced taxa, however, differed between periods, with crappies dominating backwater catches in the earlier period, and yellow perch dominating in 1995.

General patterns of assemblage composition also varied among individual sample locations. In all years, fish abundance and species richness were highest at Plymouth Slough, and lowest at the forebay location, which was characterized by catches of only a few numerically dominant taxa.

TABLE 1. Scientific and common names of resident fishes collected by beach seining in the John Day Reservoir, Columbia River, during 1984, 1985, and 1995. [a] = Introduced species.

Scientific name	Common name
Cyprinidae	Carps and minnows
Acrocheilus alutaceus	Chiselmouth
Carassius auratus	Goldfish[a]
Cyprinus carpio	Common carp[a]
Mylocheilus caurinus	Peamouth
Ptychocheilus oregonensis	Northern pikeminnow
Rhinichthys osculus	Speckled dace
Richardsonius balteatus	Redside shiner
Catostomidae	Suckers
Catostomus columbianus	Bridgelip sucker
Catostomus macrocheilus	Largescale sucker
Ictaluridae	Bullhead catfishes
Ameiurus natalis	Yellow bullhead[a]
Ameiurus nebulosus	Brown bullhead[a]
Ictalurus punctatus	Channel catfish[a]
Salmonidae	Trouts
Prosopium williamsoni	Mountain whitefish
Percopsidae	Trout-perches
Percopsis transmontana	Sand roller
Gasterosteidae	Sticklebacks
Gasterosteus aculeatus	Threespine stickleback
Cottidae	Sculpins
Cottus spp.	Sculpin spp.
Centrarchidae	Sunfishes
Lepomis gibbosus	Pumpkinseed[a]
Lepomis macrochirus	Bluegill[a]
Micropterus dolomieu	Smallmouth bass[a]
Micropterus salmoides	Largemouth bass[a]
Pomoxis annularis	White crappie[a]
Pomoxis nigromaculatus	Black crappie[a]
Percidae	Perches
Perca flavescens	Yellow perch[a]
Stizostedion vitreum vitreum	Walleye[a]

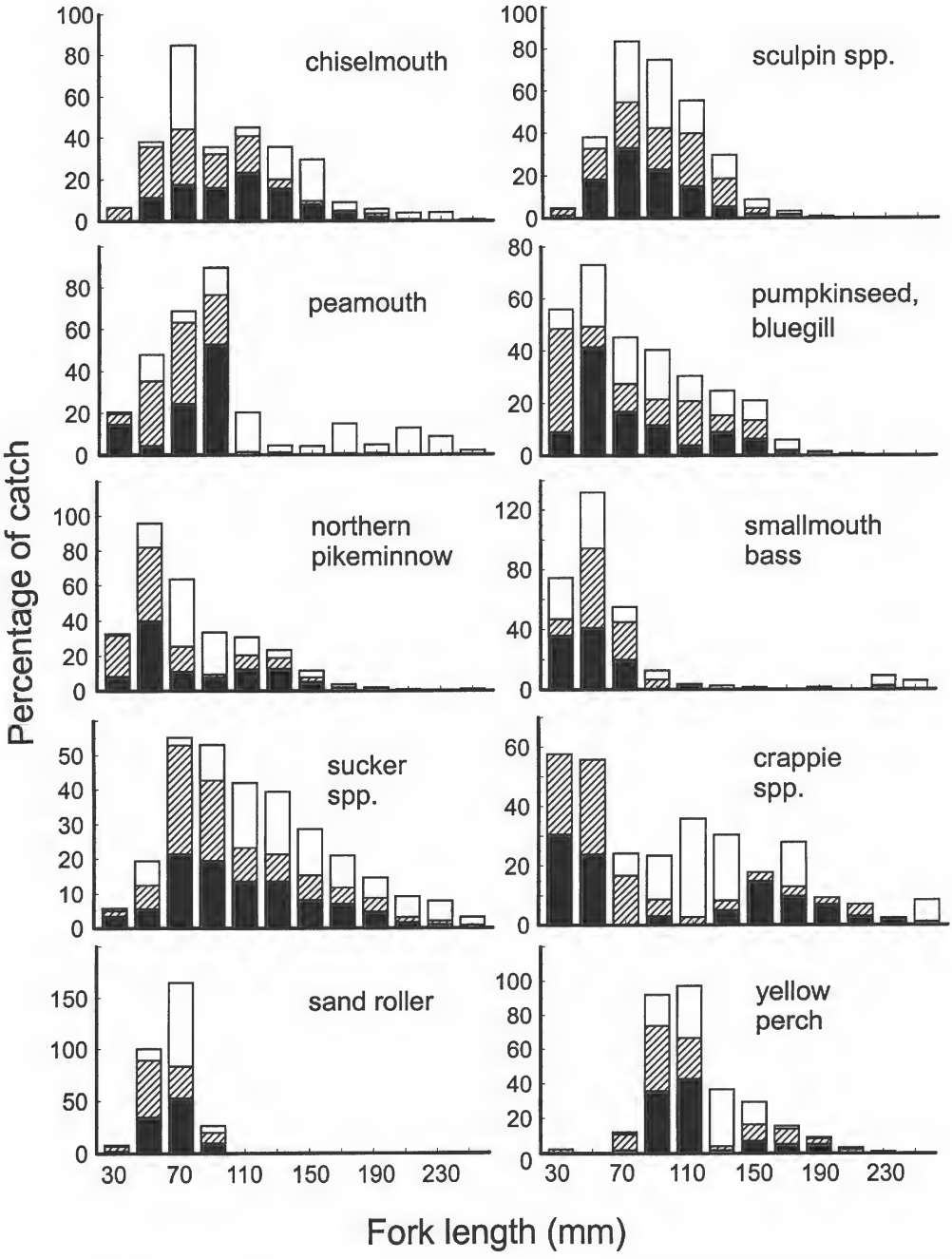


Figure 2. Length-frequency distributions of the 10 most abundant taxa collected by beach seining during May-September 1984 (black), 1985 (lines), and 1995 (white).

TABLE 2. Percent (%) composition of the 10 overall most abundant taxa collected by beach seining in the John Day Reservoir, Columbia River, during May-September 1984-1985 and 1995 in main-channel (MC) and backwater (BW) locations. Numbers of fish are sums of the 10 most abundant taxa only. CPUE=catch per unit effort. [a] = Introduced species.

	1984-1985		1995	
	MC	BW	MC	BW
Overview				
Number of hauls:	122	64	136	37
Number of fish:	14,102	12,743	5,701	3,739
CPUE:	116	199	42	101
% Composition				
Chiselmouth	15.3	1.7	2.4	3.3
Peamouth	2.3	11.8	8.1	12.5
Northern pikeminnow	13.3	18.6	6.7	29.9
Suckers	36.8	37.0	12.1	8.5
Sand rollers	28.3	3.3	17.5	9.0
Sculpins	3.0	1.2	20.8	3.8
Pumpkinseed, bluegill[a]	0.2	5.0	7.3	4.4
Smallmouth bass[a]	0.4	1.9	2.2	6.2
Crappies[a]	0.2	17.0	0.4	0.1
Yellow perch[a]	0.2	2.5	22.4	22.3

Although patterns of relative abundance varied somewhat between locations, during 1984 and 1985 a core group of native taxa (cyprinids, suckers, and sand rollers) dominated the catch at all individual locations except Paterson Slough, where introduced sunfishes and yellow perch made up a large percentage of the catch. Conversely, at nearly all main-channel sample locations during 1995, a larger percentage of the catch comprised introduced taxa, particularly yellow perch, than in the earlier sample. This shift in catch composition was greatest at the lower pool location where introduced taxa constituted 61% of the 1995 catch.

Assemblage Structure

Within-Year Comparisons

Based on rank correlation coefficients, catch composition did not vary greatly between seasons in main-channel habitats. Agreement between spring and summer resident fish taxa ranks of main-channel catches (pooled across locations) was strong (r_s = 0.76-0.97) and significant ($P < 0.05$) during all 3 yrs of the study (Table 3). Likewise, taxa ranks were concordant among seasonal catches at individual main-channel locations except at the lower pool in 1984 and the forebay in 1995. In contrast to the general pattern at main-channel locations, correlations between seasonal taxa ranks in backwaters (catches pooled across both backwater locations) were low and not significant except during 1995 (Table 3). Similarly, agreement between assemblages was low and not significant (r_s range = -0.18 - 0.33) at individual backwater locations between spring and summer in both 1984 and 1985, but seasonal assemblages were similar in 1995 (Table 3). In backwaters during 1984 and 1985, ranked abundances of some native taxa

TABLE 3. Seasonal comparisons (spring and summer) of fish assemblages in the John Day Reservoir, Columbia River, in 1984, 1985, and 1995. Agreement between seasonal assemblages was calculated with Spearman's rank correlation coefficient (r_s) on the rank ordered abundances of the 10 overall most abundant taxa for each comparison. Proportional similarity indices (PSI) were calculated on the catch of all taxa. * = $P < 0.05$.

Year and location	r_s	PSI
1984		
Forebay	0.86*	0.83
Lower pool	0.25	0.45
Upper pool	0.82*	0.77
Tailrace	0.80*	0.62
Paterson Slough	0.22	0.29
Plymouth Slough	0.33	0.76
Pooled data		
All main-channel locations	0.97*	0.82
All backwater locations	0.37	0.71
1985		
Forebay	0.80*	0.95
Lower pool	0.71*	0.73
Upper pool	0.87*	0.68
Tailrace	0.81*	0.36
Paterson Slough	-0.18	0.22
Plymouth Slough	-0.07	0.28
Pooled data		
All main-channel locations	0.85*	0.66
All backwater locations	-0.21	0.22
1995		
Forebay	0.54	0.70
Lower pool	0.91*	0.76
Upper pool	0.92*	0.56
Tailrace	0.77*	0.69
Paterson Slough	0.78*	0.77
Plymouth Slough	0.72*	0.71
Pooled data		
All main-channel locations	0.76*	0.73
All backwater locations	0.73*	0.79

(peamouth [*Mylocheilus caurinus*], northern pikeminnow, suckers, and sand rollers) consistently declined from spring to summer, and ranked abundances of introduced sunfishes increased.

Proportional similarity indices (PSI) exhibited moderate agreement with rank correlation measures of assemblage similarity at the seasonal level of comparison (Table 3). Only six of 16 significant rank correlations had PSI values of < 0.70, with only two of these < 0.62, indicating at least moderate similarity for nearly all seasonal comparisons. An additional three comparisons lacked significant concordance among ranks, but had relatively high (> 0.70) PSI values.

Annual Comparisons

Annual comparisons of main-channel fish faunal composition revealed few differences between 1984 and 1985. The correlation between rank orders (catches pooled across all main-channel locations) was significant ($P < 0.05$), indicating strong concordance between years (Table 4). Annual comparisons of assemblage structure at individual main-channel locations also demonstrated strong agreement between 1984 and 1985. Backwater faunal composition, in contrast, was dissimilar between the 2 yrs at individual locations (Table 4). The rank correlation of annual catches pooled across all backwaters was low but significant ($P < 0.05$). In both years, suckers dominated backwater catches. Differences in catch composition (catches pooled across both backwaters) were largely due to changes in the rank abundances of introduced sunfishes and yellow perch.

TABLE 4. Annual (1984 compared to 1985) and long-term (pooled 1984-1985 compared to 1995) comparisons of fish assemblages in the John Day Reservoir, Columbia River. Agreement between assemblages was calculated with Spearman's rank correlation analysis (r_s). Analyses were conducted on the rank ordered abundances of the 10 overall most abundant taxa for each comparison. Proportional similarity indices (PSI) were calculated on the catch of all taxa. * = $P < 0.05$.

Time period and location	r_s	PSI
Annual		
Forebay	0.74*	0.70
Lower pool	0.85*	0.86
Upper pool	0.89*	0.86
Tailrace	0.84*	0.65
Paterson Slough	0.38	0.74
Plymouth Slough	0.43	0.61
Pooled data		
All main-channel locations	0.85*	0.73
All backwater locations	0.56*	0.63
Long term		
Forebay	0.29	0.21
Lower pool	-0.44	0.30
Upper pool	0.24	0.57
Tailrace	0.47	0.50
Pooled data		
All main-channel locations	0.07	0.44

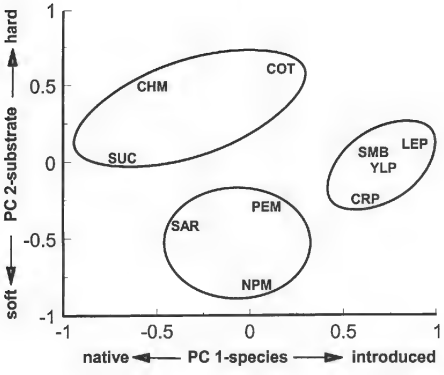
Long-Term Comparisons

Long-term comparisons of fish taxa ranks indicated that main-channel shoreline fish faunal structure changed greatly between the earlier period (pooled 1984-85 catch) and 1995. Large changes in catch composition were indicated by low ($r_s \leq 0.47$) and nonsignificant correlations at all main-channel locations (Table 4). Major shifts in faunal composition between the two periods (catches pooled across all main-channel locations) resulted from declines in the rank abundance of native suckers and cyprinids (chiselmouth and northern pikeminnow) and increases in ranks of sculpins, and introduced sunfishes and yellow perch. Similar long-term changes in taxon contributions to assemblage structure occurred at individual main-channel locations.

Annual and long-term PSI values were consistent with rank concordance measures of assemblage similarity (Table 4). Annual comparisons of assemblage structure with significant Spearman's rank correlations always had PSI values of ≥ 0.65, whereas most long-term comparisons of main-channel assemblage structure (all correlations were nonsignificant) had PSI values ≤ 0.5. Proportional similarity index values, however, indicated higher similarities at individual backwater locations between 1984 and 1985 than did rank concordance measures of annual similarity.

Ordinations of Taxon Associations and Sample Location Relationships

A plot of fish taxa loadings on the first two principal component (PC) axes revealed three relatively well-defined, ecologically interpretable fish taxa associations (Figure 3). The first component explained 30% of the variance in the relative abundance data and separated native (negative or



CHM = chiselmouth	LEP = pumpkinseed, bluegill
PEM = peamouth	SMB = smallmouth bass
NPM = northern pikeminnow	CRP = crappie spp.
SUC = sucker spp.	YLP = yellow perch
SAR = sand roller	
COT = sculpin spp.	

Figure 3. Taxa loadings on the first two axes of a principal components (PC) analysis of fish relative abundance. Fishes were collected by beach seining during May-September 1984, 1985, and 1995.

low positive loadings on PC 1) from introduced taxa (loadings ≥ 0.60 on PC 1). The second component accounted for 21% of the variation in the data set and separated taxa (high positive loadings on PC 2) that were generally associated with hard substrate (gravel-cobble) habitats from taxa associated with soft (fines-sand) sediments. The three major groups of taxa were a native association of chiselmouth, suckers, and sculpins, a native association of peamouth, northern pikeminnow, and sand rollers, and a third group of introduced fishes: pumpkinseed (*Lepomis gibbosus*), bluegill (*L. macrochirus*), smallmouth bass, white crappie (*Pomoxis annularis*), black crappie (*P. nigromaculatus*), and yellow perch.

An ordination of monthly (by year) location scores on the first two principal components exhibited both spatial and temporal (seasonal and annual) trends in clusters of sampling units. Temporal patterns in groupings of monthly samples concurred closely with the seasonal, annual, and long-term measures of concordance (Figure 4). There was generally little separation of monthly location scores from within a year at individual main-channel locations. Monthly scores at individual main-channel locations also did not differ greatly between 1984 and 1985, however, 1984 and 1985 location scores typically differed substantially from 1995 scores. Monthly backwater scores showed an overall greater amount of variability than main-channel scores, both within a year and between years, which is consistent with the rank measures of assemblage similarity (Table 4).

The fish assemblages present at a location influenced the groupings of location scores (Figures 3, 4). For example, introduced taxa had comparatively high positive loadings on PC 1; thus, monthly samples with high relative abundances of introduced taxa have higher scores on PC 1. Samples from Paterson Slough generally had the highest positive scores on the first component, particularly during August 1984 and 1985, and May and June 1995 (we were unable to sample in this area after June 1995), indicating the importance of this habitat to introduced taxa (e.g., sunfishes and yellow perch). In Plymouth Slough, high relative abundances of young-age classes of peamouth and northern pikeminnow contributed to relatively large negative monthly scores on PC 2, regardless of year (Figure 4). An increased relative abundance of introduced taxa in Plymouth Slough during August 1985, and during July and August 1995, shifted location scores to the right of the ordination. Positive location scores on PC 1 in 1995 indicate the increasing importance of introduced taxa to assemblage structure at nearly all main-channel locations. The main-channel area with the highest average monthly PC 1 scores in 1995 was the lower pool location, where more than half of all fishes collected were introduced. The main-channel area with the lowest average scores on PC 1 in 1995 was the tailrace location, an area that harbored a mostly native fish species assemblage. Monthly tailrace location ordination scores also exhibited the least amount of separation from 1984-1985 ordination scores; this area additionally had the highest, but still low and nonsignificant, measure of concordance over the long-term sampling period (Table 4).

Water Temperature and Discharge Patterns

Temperature and discharge conditions in 1995 were generally intermediate between 1984 and 1985 (Figure 5). Discharge was lowest in 1985, and highest in 1984, with peaks in the hydrograph occurring in all years during late May or early

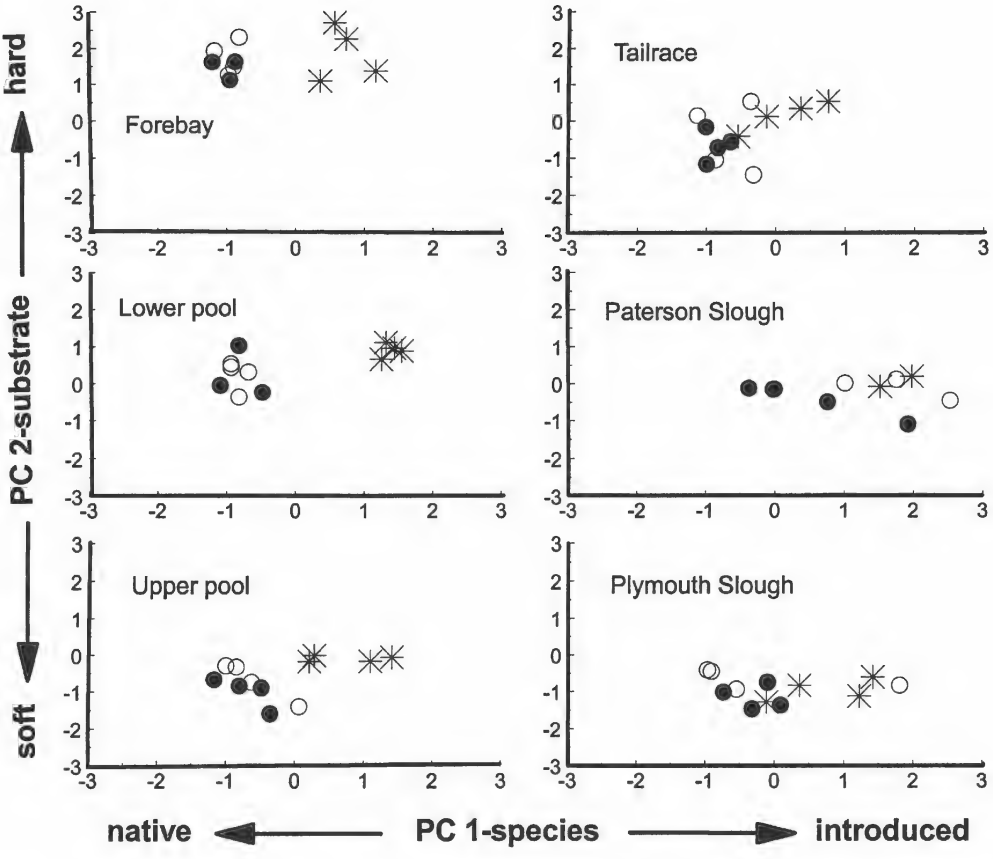


Figure 4. Principal components (PC) ordination of monthly location scores for six major beach seine sampling locations. The PC analysis was conducted on a correlation matrix of the monthly catch of the 10 overall most abundant fish taxa in beach seine samples collected during spring and summer 1984, 1985, and 1995. Black circles represent scores for 1984 monthly samples, white circles represent 1985, and stars represent 1995.

June. Annual water temperature and discharge patterns were inversely related. Temperatures were highest in 1985 and lowest in 1984. Water temperatures early in 1995 were slightly higher (typically $\leq 1.5^{\circ}$ C) than temperatures in 1985 until early June, and then were intermediate. Within a year, main-channel temperatures were highest in late July or early August, with peaks ranging from 21.7 to 23.3° C.

Discussion

We detected both seasonal and long-term variations in the makeup of shallow water fish assemblages within the John Day Reservoir. Seasonally, the proportion of introduced sunfishes in backwaters increased from spring to summer during 1984 and 1985. This increase is likely related to environmental conditions in these areas. Both slough locations are shallow, well vegetated, and have low water exchange rates resulting in summer water temperatures often several degrees higher than nearby main-channel habitats with greater water exchange (Gadomski and Barfoot 1998). These higher temperatures are nearer to optimal for some introduced species such as bluegill and smallmouth bass (Horning and Pearson 1973, Lemke 1977). Temperature is associated with seasonal movements and distributions of fishes

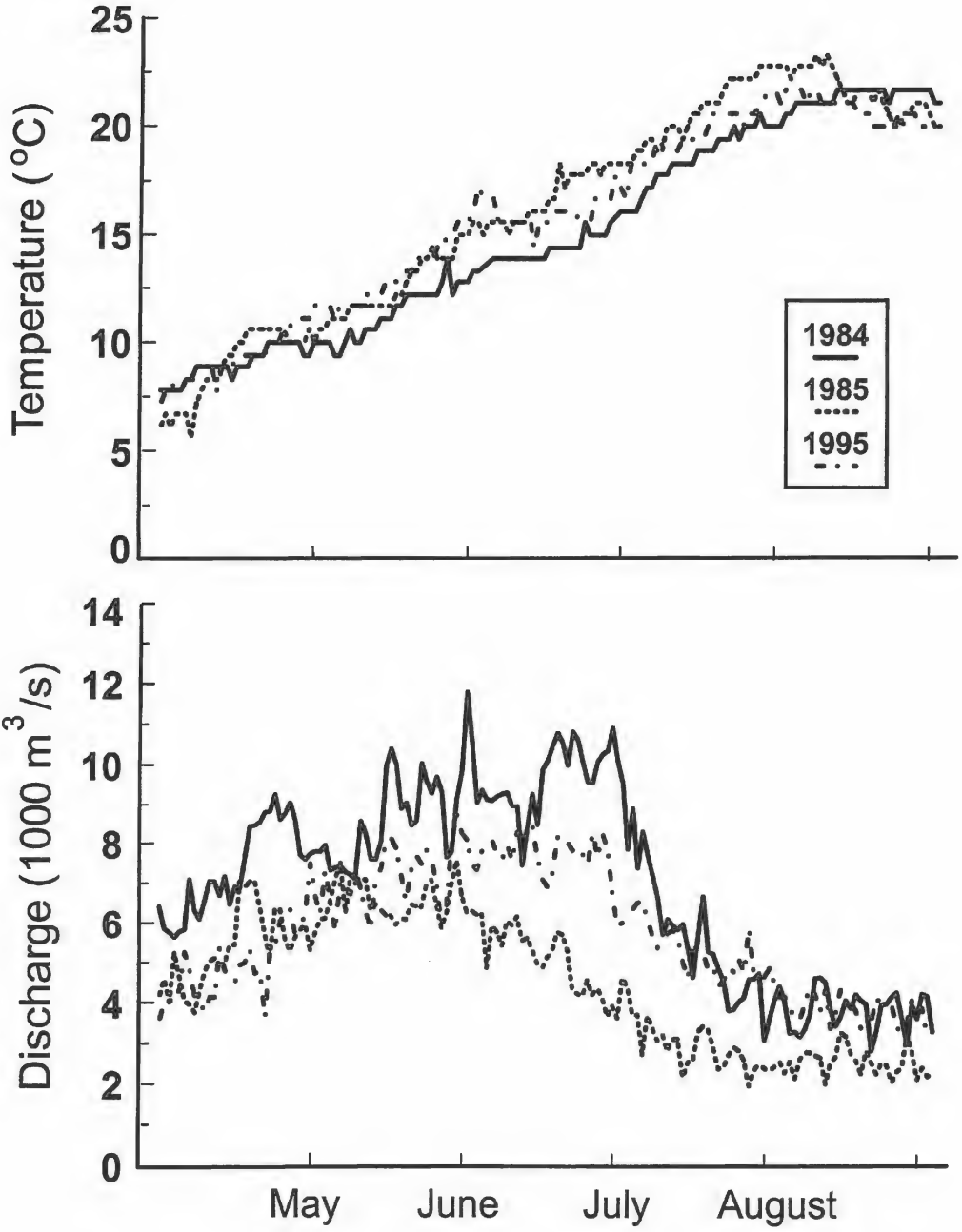


Figure 5. Columbia River temperature and discharge regimes at McNary Dam during spring and summer 1984, 1985, and 1995. Data were obtained from StreamNet 2001.

in lentic habitats (Hall and Werner 1977, Hubert and Lackey 1980, Tufescu 1994, Garret and Bennett 1995). Thus, higher late summer temperatures may have caused native taxa to shift habitat use out of backwaters, while introduced warmwater taxa may have moved into or remained in these areas.

We also observed substantial long-term changes in shallow-water fish assemblages of the John Day Reservoir. At our scale of examination, fish catch composition between 1984 and 1985 was similar, but was different from 1995 catches. Two native taxa assemblages dominated the catch in the earlier 1984-1985 sampling period and appeared to be generally separated along a habitat gradient of hard (gravel and cobble) versus soft (silt and sand) substrate types. The hard substrate assemblage comprised chiselmouth, suckers, and sculpins. The chiselmouth is a native herbivorous cyprinid that is strongly associated with hard substrates from which it scrapes plant material (Moodie and Lindsey 1972), and sculpins as a group are generally lithophilic. Chiselmouth and sculpins were typically most abundant in low-velocity cobble habitats of the forebay sample location.

The second native species association dominant in 1984-1985 was most abundant over soft substrates and contained two cyprinids (peamouth and northern pikeminnow) and sand rollers. Younger age classes of peamouth and northern pikeminnow rear in sandy low-gradient habitats (Beamesderfer 1992, Gadomski et al. 2001), while sand rollers are particularly abundant over sandy bottoms at nighttime (Gray and Dauble 1976). The highest abundances of these three species were at Plymouth Slough sites and some upper pool sample locations with soft substrates.

The third species assemblage we identified was generally not abundant in 1984-1985, except in the Paterson Slough, but in 1995 became increasingly more important to fish assemblage composition at nearly all main-channel locations. This assemblage comprised bluegill, pumpkinseed, smallmouth bass, white and black crappies, and yellow perch. All of these taxa are introduced and typical of lake-like habitats, with the exception of smallmouth bass, which occurs in both still and moving waters (Edwards et al. 1983).

The long-term differences in fish assemblages we observed may be due to simple year-to-year variation, decadal environmental differences, or to persistent habitat changes related to reservoir aging. The three years of sampling did not allow us to assess year-to-year variation in any detail, however. Similar studies in the basin are unavailable for comparison with ours, and information is minimal on the temporal variability and structure of shallow-water fish assemblages in impoundments (Hubert and O'Shea 1991).

General environmental conditions in the John Day Reservoir differed between the early 1980's and 1990's, which could be responsible for observed changes in fish fauna. Discharge regimes in the Columbia River associated with the two sample periods were dissimilar (Figure 6). Discharge has been shown to covary with spring and summer water temperatures (Quinn and Adams 1996), turbidities, and reservoir water-retention rates. Conditions leading up to and encompassing the earlier 1984-1985 sampling period were primarily characterized by above average annual discharge, while average annual discharge for the later period was generally below the long-term average (Figure 6). Additionally, in 1983 a water budget was adopted by the Columbia Basin hydrosystem. The goal has been to augment river flows during spring to increase down-river migration rates of juvenile salmonids, but this also has resulted in lower than average summer flows (Berggren and Filardo 1993).

Discharge and temperature regimes, in particular, can influence annual variations in reservoir fish assemblages by differentially influencing year-class strengths of individual species or groups of species with similar life histories. For example, Kallemeyn (1987) found a positive relationship between percid year-class strengths and thermal regimes, with the strongest year classes being produced in years with comparatively high, stable water temperatures. Elevated turbidities (Mitzner 1991) and high reservoir flushing rates (Walburg 1971, Beam 1983, Maceina and Stimpert 1998), both correlates of high reservoir inflows, can be negatively related to crappie recruitment success. Thus, the high discharge regime during the early 1980's may have favored the reproductive success of native taxa in the John Day Reservoir, while several successive years of low precipitation and runoff in the early 1990's might have favored introduced taxa.

Alternatively, the long-term changes that we observed in fish assemblages may be more persistent and less related to short-term, climatically

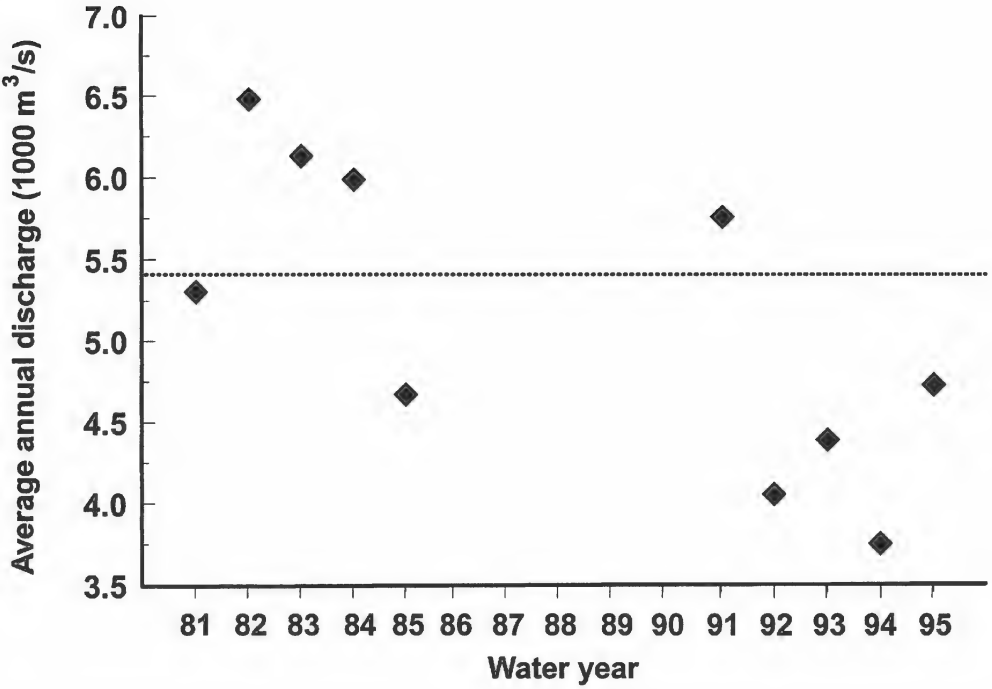


Figure 6. Mean annual discharge at The Dalles Dam, Columbia River, during five-year intervals before and during each of the two fish sampling periods (1984-1985; 1995). The dashed horizontal line indicates the long-term average annual discharge at The Dalles Dam. Data were obtained from the USGS (2001).

influenced variations in distribution and reproductive success. The trends we observed in 1995 (i.e., an increasing relative abundance of introduced species more typically associated with lake-like habitats) are consistent with long-term, post-impoundment patterns of assemblage change described by Li et al. (1987) for the Snake and Columbia rivers, suggesting that such changes can be expected in John Day Reservoir near-shore fish assemblages. Similar large-scale persistent shifts in post-impoundment fish assemblage composition have also been described elsewhere. For example, in a Colorado Reservoir, species composition changed substantially over a 6-yr period from an assemblage dominated by native riverine species to one primarily of introduced taxa adapted to lentic conditions (Martinez et al. 1994).

The abundance of aquatic macrophytes in John Day Reservoir, a habitat feature associated with reservoir aging, is one mechanism that likely influenced fish assemblage composition over the long term. An increase in the abundance of aquatic macrophytes in impoundments over time is a predictable outcome of siltation due to both anthropogenic induced and natural reservoir aging processes (Kimmel and Groeger 1986). We observed an abundance of aquatic macrophytes in many shallow areas of John Day Reservoir during 1995, whereas investigators who conducted the earlier sampling (1984-1985) reported some beds of macrophytes, primarily pondweed (*Potamogeton* spp.), but at lower densities (Michael J. Parsley, USGS, personal communication). In Paterson Slough, for example, macrophyte abundance (primarily milfoil) prevented us from sampling with a beach seine after mid-summer in 1995. Rooted aquatic vegetation can play a key role in altering the ecology of shallow habitats by changing water circulation patterns, dissolved oxygen, pH, and the temperature of localized areas (Carter et al. 1991). In Columbia River impoundments, these changes may favor non-native lentic taxa over

native riverine species. Macrophyte beds also create structurally complex spawning, rearing, and foraging habitats (Kilgore et al. 1989, Weaver et al. 1997), which are well-suited to many of the introduced fish species (e.g., bluegill, pumpkinseed, black crappie, and yellow perch) present in John Day Reservoir.

Since shallow littoral reservoir habitats are rearing areas for anadromous salmonids, particularly fall chinook salmon (*Oncorhynchus tshawytscha*) post-impoundment shoreline habitat and fish assemblage changes could be affecting the suitability of reservoirs for salmonid production. However, relatively little is known about the complex relationship between reservoir food webs, habitat conditions, introduced fish taxa, and juvenile salmonids. Many introduced fish species now abundant in shoreline and backwater areas of the John Day Reservoir could directly prey upon or compete with juvenile salmonids, although these relationships have generally not been studied. Earlier predation studies (Poe et al. 1991, Vigg et al. 1991) in John Day Reservoir did not identify sunfishes or yellow perch as important predators of juvenile salmonids, although crappie and yellow perch diets in some locations of the impounded lower Snake River comprised 20-25% juvenile salmonids (Bennett 1999).

More information on how short- and long-term changes in near-shore habitats and fish assemblages affect anadromous salmonids would aid ongoing recovery efforts in the highly regulated Snake and Columbia Rivers. The last major population of main-stem Columbia River fall chinook salmon is in the unimpounded Hanford Reach, an area where introduced taxa represent only a minor component of the fish assemblage (Li et al. 1987). This suggests that management actions that may partially restore riverine conditions and natural fish assemblages to impounded reaches of the Snake and Columbia rivers may ultimately benefit salmonid production.

Acknowledgements

We thank Jennifer Kelly for field assistance, and Samuel C. Lohr and two anonymous readers for reviewing the manuscript. This work was funded by the Army Corps of Engineers.

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Received 14 May 2001
Accepted for publication 23 December 2001

Matthew G. Mesa,[1] **Lisa K. Weiland,** U.S. Geological Survey, Biological Resources Division, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Rd., Cook, Washington 98605

and

Paul Wagner,[2] Washington Department of Fish and Wildlife, 500 N. Moraine St., Suite 1200E, Kennewick, Washington 99336

Effects of Acute Thermal Stress on the Survival, Predator Avoidance, and Physiology of Juvenile Fall Chinook Salmon

Abstract

We subjected juvenile fall chinook salmon from the Hanford Reach of the Columbia River to acute thermal stressors in the laboratory that were derived from field data. We assessed the effects of thermal stress on: (1) the extent of direct mortality; (2) the vulnerability of fish to predation by smallmouth bass; and (3) some general physiological stress responses and synthesis of heat shock protein 70 (hsp70). Thermally-stressed fish showed little direct mortality and no increases in vulnerability to predation. However, these fish showed transient increases in plasma concentrations of cortisol, glucose, and lactate, and a dramatic (25-fold higher than controls) and persistent (lasting 2 wk) increase in levels of liver hsp70. Our results indicate that exposure of Hanford Reach juvenile fall chinook salmon to such stressors did not lead to significant increases in direct mortality or vulnerability to predation, but did alter physiological homeostasis, which should be of concern to those managing this resource. Because our fish received only a single exposure to one of the stressors we examined, we are also concerned about the consequences of exposing fish to multiple, cumulative stressors—a likely scenario for fish in the wild.

Introduction

The Hanford Reach, the last free-flowing section of the Columbia River, supports a large and important population of wild fall chinook salmon (*Oncorhynchus tshawytscha*). Recently, concerns have been raised about potential losses of these fish due to river level fluctuations resulting from power peaking operations at dams upstream of the reach. Rapid fluctuations in river level can cause stranding (the trapping of fish on or within the unwatered substrate as a result of receding river level) of juvenile fall chinook salmon and lead to direct mortality. For example, during spring and early summer weekly sampling of fall chinook salmon on the Hanford Reach in 1998, almost 8,000 fish were found stranded and dead along the shoreline (Nugent et al. 2001a).

Besides stranding, fish can also become entrapped in isolated backwaters that form when water rapidly recedes. In the spring and summer of 1998, the Washington Department of Fish and Wildlife (WDFW) estimated that at least 24,000 juvenile fall chinook salmon were entrapped for various lengths of time in isolated pools (Nugent et al. 2001a). In 1999, using random plot sampling and computer modeling, they estimated that at least 125,000 fall chinook salmon perished due to stranding and entrapment (Nugent et al. 2001b). Although such entrapment may not cause rapid mortality, it may lead to delayed mortality from two indirect sources: predation or alterations in performance caused by sublethal heat stress. We have observed predation by birds and fish on juvenile salmon entrapped in pools on several occasions in the Hanford Reach.

Alterations in performance of fish caused by sublethal heat stress is a more insidious and potentially devastating effect of entrapment. Fish entrapped in backwaters on the Hanford Reach can experience a unique type of thermal stressor, typically consisting of exposure to gradual (i.e., over several hours) and extreme (i.e., >10°C above ambient temperatures) increases in temperature followed by an abrupt decrease in temperature when they are liberated into the main river as water levels rapidly rise. Sublethal, acute thermal shocks increase the vulnerability of fish to predation (Sylvester 1972, Coutant 1973, Yocom and Edsall 1974, Deacutis 1978), cause a variety of physiological disturbances in fish including increases

[1]Author to whom correspondence should be addressed. E-mail: matt_mesa@usgs.gov

[2]Present address: Golder Associates, P.O. Box 73, Plymouth, WA 99346

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in plasma glucose and cortisol (Wedemeyer 1973, Strange et al. 1977, Crawshaw 1977, 1979, Bailey et al. 1991, Soncini and Glass 1997), and elicit the rapid synthesis of stress proteins that play a role in repair and protection from environmentally induced cellular damage (Sanders 1993, Iwama et al. 1998). However, information from these studies may not apply to fall chinook salmon in the Hanford Reach because of their species, age, and the unique nature of the stressor experienced by these fish. Clearly, such a stressor has the potential to alter behavioral, physiological and cellular mechanisms that could lead to delayed or indirect mortality of the fish. An understanding of the effects of acute heat stress on juvenile fall chinook salmon is necessary to assess the impacts of entrapment on populations of these fish in the Hanford Reach, and it will also contribute to knowledge of thermal stressors in general.

In this study, we exposed juvenile fall chinook salmon from the Hanford Reach to four heat stress scenarios in the laboratory that were derived from field data. We then assessed the effects of thermal stress on: (1) the extent of direct mortality; (2) the vulnerability of fish to predation by smallmouth bass (*Micropterus dolomieui*); and (3) some general physiological stress responses and synthesis of heat shock protein 70 (hsp70).

Methods

Test fish

Subyearling fall chinook salmon were collected by seine from the Hanford Reach during April and May in 1998 and 1999. Fish were transported to our laboratory in a truck equipped with a large, insulated aluminum tank and aerated water. They initially averaged 38.4 ± 0.6 mm in length and 0.7 ± 0.1 g in weight. The fish were placed in 1400 L flow-through circular tanks, reared outdoors under ambient photoperiod, and fed twice daily (at a ration of 3-4 % body weight per day) with blood worms for the first month and a commercial starter feed thereafter.

Sixteen smallmouth bass (mean length = 306 ± 6 mm; weight = 457 ± 27 g) were used in our predation trials and were collected by angling from the lower Yakima River, Washington, in 1998 and by electrofishing in the Columbia River in 1999. They were transported to our laboratory as previously described and placed four fish per tank in each of two 3.75-m-diameter, 1-m-deep circular tanks. The tanks were lined with gravel and cobble substrates and included four pieces of 0.25-m-long, 15-cm-diameter PVC pipe randomly scattered along the bottom to serve as cover. These tanks were indoors and served as our predation arenas. They were surrounded with curtains to minimize outside disturbance and under an ambient photoperiod simulated with 25 W incandescent bulbs and timers to produce a gradual intensity dawn and dusk. Predators were fed a maintenance diet of juvenile chinook salmon (about two fish per predator every 2-3 d). All fish were acclimated to and held in well water heated to 12°C, which was representative of river temperatures in the Hanford Reach during spring (Nugent et al. 2001a, b). The water was heated using large, single-pass electric heaters and excess dissolved gas generated by heating was dissipated by a packed column.

Direct mortality bioassays

We used fall chinook salmon in these tests, which were conducted during June and July in 1999, that had a mean length of 55.5 ± 0.4 mm and a weight of 1.5 ± 0.1 g (n = 160). Four groups of 20 fish were serially removed from their holding tank and transferred to one of four 0.61-m-diameter circular test tanks. Two of these tanks contained a 2000 W immersion heater connected to an electronic controller that was used to produce the thermal stressors (described below). Our thermal stressors were modeled after data from thermographs placed in entrapment pools in the Hanford Reach (see examples in Figure 1A; Nugent et al. 2001a, b). All tanks received the same water as the holding tanks with an inflow of about 1 L/min and a volume of 104 L. Densities in the test tanks were ~ 0.28 g/L. Fish were held undisturbed for at least 2 d prior to starting the bioassays.

At the start of a bioassay, fish in the two heated tanks were designated as treatment fish, whereas fish in the other two tanks remained at 12°C during the experiment and were designated as controls. At 0700, treatment fish were subjected to one of four thermal stressors in separate trials (Figure 1B). Stressor 1 consisted of heating the water from 12°C to 26°C at a rate of 2°C/hr, followed by a decrease to 12°C in about 1 hr. Stressor 2 was the same, except that the temperature increase was 4°C/hr. For these stressors, fish remained at 26°C for about 10-15 min. Stressor 3

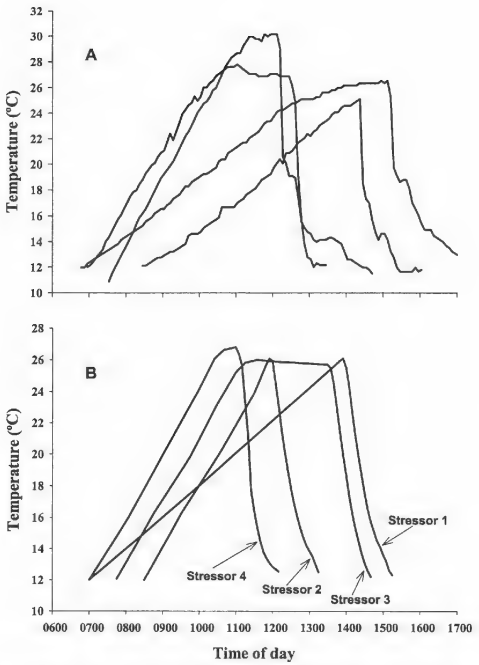

Figure 1. (A) Temperature profiles in selected entrapment pools on the Hanford Reach during spring 1998. Data were taken from thermographs placed in the pools. (B) Thermal stressors used in laboratory experiments. Curves were spline-fit to thermograph data from several tanks during our study. Starting times for the curves were staggered to facilitate graphical representation.

was the same as Stressor 2, except that fish remained at 26°C until about 25% of the fish showed disequilibrium or died. Stressor 4 was also similar to Stressor 2, except that the maximum temperature was increased to approximately 27°C. For all stressors, when heating was complete, the heaters were turned off and a 6-7°C inflow of water was used to cool water temperature to 12°C in about 1 hr. After the treatments, fish remained in their tanks at 12°C for a period of 5 d. Miniature temperature loggers in each tank recorded water temperature every 5 min during application of the stressor and every hour thereafter. At each hour during the bioassay and three times a day thereafter, we removed and tallied dead fish. In total, we conducted one complete trial for each stressor consisting of two replicate tanks each of treatment and control fish.

Predation Trials

We conducted predation trials during two years, from July through September in 1998, and from June through July in 1999. In 1998, fall chinook salmon had a mean length of 77.0 ± 0.4 mm and a weight of 4.7 ± 0.1 g ($n = 279$); in 1999, fish had a mean length of 56.0 ± 0.2 mm and a weight of 1.6 ± 0.1 g ($n = 170$). For a trial, four groups of 15-20 fish were anesthetized using 50 mg/L tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate. Two groups were designated as control and two were designated as treatment. We randomly selected and marked two groups (i.e., either control or treatment fish) by clipping the adipose fin with surgical scissors, whereas the other groups were sham marked by simply holding them out of the water for a sufficient period. Fourteen marked fish were placed in each of two control and treatment tanks as described in the mortality bioassays. Fish were held in these tanks for 2-3 d before being subjected to thermal stress.

On the morning of a predation trial, fish in the treatment tanks were subjected to one of two thermal stressors. Control fish and the predators always remained at 12°C. In 1998, we conducted eight trials using Stressor 1 and 12 trials using Stressor 2. In 1999, we conducted 12 trials using Stressor 1. Immediately after fish were exposed to thermal stress (i.e., when water temperature in the treatment tanks was back at 12°C), water level in all tanks was dropped to approximately 16 L. Fish were then released into a 19 L bucket below the tanks. Equal numbers of control and treatment fish were mixed in one bucket and poured into a predation tank. Smallmouth bass were allowed to consume juvenile salmon until 50% of the prey were eaten or 2 hr had passed, whichever occurred first. We observed fish behavior and estimated the number of prey eaten. Afterwards, the remaining prey were seined from the tanks and placed in a lethal dose (200 mg/L) of MS-222. Lengths and weights were recorded and fish were identified as treatment or control based on the presence of an adipose fin.

We analyzed these data in a manner identical to that of Mesa (1994). We first subjected data to a heterogeneity χ^2 analysis to determine if the individual tests were homogenous (Sokal and Rohlf 1981). Chi-squared goodness-of-fit tests were then used on pooled data to determine if predation was random (i.e., 50:50) on treated versus control fish.

Because the χ^2 test has low statistical power (i.e., low probability of correctly rejecting the null hypothesis) when relatively small sample sizes are used, we set the significance level at $P = 0.10$, the detectable difference in predation rates (i.e., the effect size) at 20%, and target sample sizes at about 180 to increase power and reduce the probability of the more serious type II error (Fairbairn and Roff 1980, Peterman 1990). Tests where less than 30% or more than 70% of the prey were eaten were excluded from the analysis for reasons discussed in Mesa and Warren (1997).

Physiology Experiment

To assess some physiological responses of juvenile fall chinook salmon to acute thermal stress, we conducted one experiment in September 1999. Fish used in this experiment had a mean length of 90.5 ± 0.5 mm and a mean weight of 7.7 ± 0.1 g (n = 126). Forty-five fish were stocked in each of two treatment tanks and two control tanks, as previously described. Fish were held in these tanks for 7 d prior to applying the stressor. At 0730 on the eighth day, fish in treatment tanks were subjected to Stressor 1; control fish remained at 12°C during the experiment. Just prior to the stressor, we removed four fish from each tank (time = 0) and also removed four fish at the following times after the start: 3 hr (midway point of the temperature increase); 7 hr (maximum temperature); 9 hr (1 hr after the rapid temperature decrease); and at 24, 72, 168, and 336 hr. All sampled fish were placed in a lethal dose of buffered MS-222, weighed and measured, and blood samples collected into ammonium-heparinized capillary tubes after the caudal peduncle was severed. Plasma was obtained by centrifugation and stored at -80°C for future analysis. Plasma cortisol was measured using an enzyme-linked immunosorbent assay (ELISA) modified from procedures described by Munro and Stabenfeldt (1984). Plasma lactate and glucose were assayed using commercial kits (Sigma Diagnostics) modified by us for use with microplates. Due to an insufficient amount of plasma, we were unable to assay all analytes from some fish. After collecting blood, we excised the liver, weighed it, wrapped it in aluminum foil and placed it in liquid nitrogen. These samples were stored at -80°C for future analysis of hsp70 expression using an ELISA (Forsyth et al. 1997).

We calculated the mean and SE for all plasma constituents at each sample period and plotted them over time. Within each sample period, we compared the means of treatment and control fish using two-sample *t*-tests for use with unequal variance. We expressed the hsp70 content of liver samples in relative units as a percentage of a positive control and analyzed the means as just described. For these tests, the level of significance was set at $P = 0.05$.

Results

Direct Mortality Bioassays

Only one control fish died during the trial exposing fish to Stressor 1, whereas only one treatment fish died during the trial assessing Stressor 2. For fish exposed to Stressor 3, about 2-2.5 hr after the maximum temperature had been reached were required for about 25% of the fish to die. Thereafter, only one treatment fish died on the second day. For fish exposed to Stressor 4, eight fish died in one treatment tank and five fish died in the other, all before the cool down phase of the stressor was complete. Thereafter, only one more treatment and one control fish died.

Predation Trials

In 1998, we conducted a total of eight trials using fish exposed to Stressor 1 with an average of 48% of fish eaten per trial. A total of 53 control and 54 treatment fish were eaten, which did not differ significantly from random (Table 1). Statistical power (to detect a 20% difference in predation rates) of the pooled χ^2 test was 0.66. Duration of predation trials ranged from 5 min to 2 hr, however the number of control and treatment fish consumed was independent of trial duration (χ^2 test of independence). There were no significant differences in length or weight of control and treatment fish measured after the trials.

Also in 1998, we conducted a total of 12 trials using fish exposed to Stressor 2 with an average of 47.5% of fish eaten per trial. There were a total of 67 control and 82 treatment fish eaten, which again was not significantly different from random (Table 2). Statistical power of the pooled χ^2 test was 0.79. Duration of predation trials ranged from 10 min to 2 hr, and again the number of control and treatment fish consumed was independent of trial duration. There was one trial with a minor (*t* test, $P < 0.05$) difference in length of control and treatment fish.

TABLE 1. Predation by smallmouth bass on juvenile fall chinook salmon acclimated to 12°C, subjected to a heating of 2°C/hr up to 26°C, and a temperature decrease within 1 hr to 12°C (i.e, Stressor 1 in Figure 1B). Data are from experiments conducted in 1998. No predation rates differed significantly from random (50:50, treatment:control).

Replicate or statistic	Number eaten		Percent eaten	Statistics	
	Control	Treatment		df	χ^2
1	7	5	43	1	0.333
2	4	6	36	1	0.400
3	11	8	68	1	0.474
4	4	7	46	1	0.818
5	10	5	54	1	1.667
6	6	8	50	1	0.286
7	5	8	46	1	0.692
8	6	7	46	1	0.077
Total	53	54		8	4.747
Pooled				1	0.009
Heterogeneity				7	4.738

TABLE 2. Predation by smallmouth bass on juvenile fall chinook salmon acclimated to 12°C, subjected to a heating of 4°C/hr up to 26°C, and a temperature decrease within 1 hr to 12°C (i.e., Stressor 2 in Figure 1B). Data are from experiments conducted in 1998. No predation rates differed significantly from random (50:50, treatment: control).

Replicate or statistic	Number eaten		Percent eaten	Statistics	
	Control	Treatment		df	χ^2
1	5	4	56	1	0.111
2	5	9	50	1	1.143
3	8	6	52	1	0.286
4	8	7	53	1	0.067
5	4	5	32	1	0.111
6	5	8	46	1	0.692
7	7	10	65	1	0.529
8	5	9	50	1	1.143
9	7	4	39	1	0.818
10	6	8	58	1	0.286
11	3	6	32	1	1.000
12	4	6	38	1	0.400
Total	67	82		12	6.586
Pooled				1	1.510
Heterogeneity				11	5.076

In 1999, we conducted a total of 12 trials using fish exposed to Stressor 1 with an average of 48.5% of fish eaten per trial. There were a total of 78 control and 83 treatment fish eaten, which was not significantly different from random (Table 3). Statistical power of the pooled χ^2 test was 0.81. Duration of predation trials ranged from 14 min to 2 hr, and again the number of control and treatment fish consumed was independent of trial duration. Although there were no significant differences in size of control and treatment fish used in these trials, fish used in 1999 were significantly smaller than those used in 1998 (t-tests, $P < 0.05$).

TABLE 3. Predation by smallmouth bass on juvenile fall chinook salmon acclimated to 12°C, subjected to a heating of 2°C/hr up to 26°C, and temperature decrease within 1 hr to 12°C (i.e., Stressor 1 in Figure 1B). Data are from experiments conducted in 1999. No predation rates differed significantly from random (50:50, treatment:control).

Replicate or statistic	Number eaten		Percent eaten	Statistics	
	Control	Treatment		df	χ^2
1	5	6	39	1	0.091
2	2	7	32	1	2.778
3	12	8	71	1	0.800
4	7	8	54	1	0.067
5	4	8	50	1	1.333
6	4	6	36	1	0.400
7	7	8	54	1	0.067
8	6	5	39	1	0.091
9	8	8	57	1	0.000
10	9	5	50	1	1.143
11	6	8	50	1	0.286
12	8	6	50	1	0.286
Total	78	83		12	7.341
Pooled				1	0.155
Heterogeneity				11	7.186

Physiology Experiment

Plasma cortisol levels in treatment fish were significantly higher than control fish prior to application of Stressor 1 (for unknown reasons) and also at 7 hr after the start of the stressor, which was the time of maximum temperature (Figure 2A). Thereafter, cortisol levels did not differ between treatment and control fish, except for a slight elevation in treatment fish at 72 hr. Plasma glucose levels increased gradually in treatment fish, peaking and becoming significantly higher than control fish only during the time of maximum temperature (Figure 2B). Control fish did show a dramatic and inexplicable increase in glucose levels at 9 hr. Lactate levels in treatment fish showed about a threefold increase during application of the stressor and were significantly higher than control fish at 7 and 9 hr (Figure 2C). Plasma

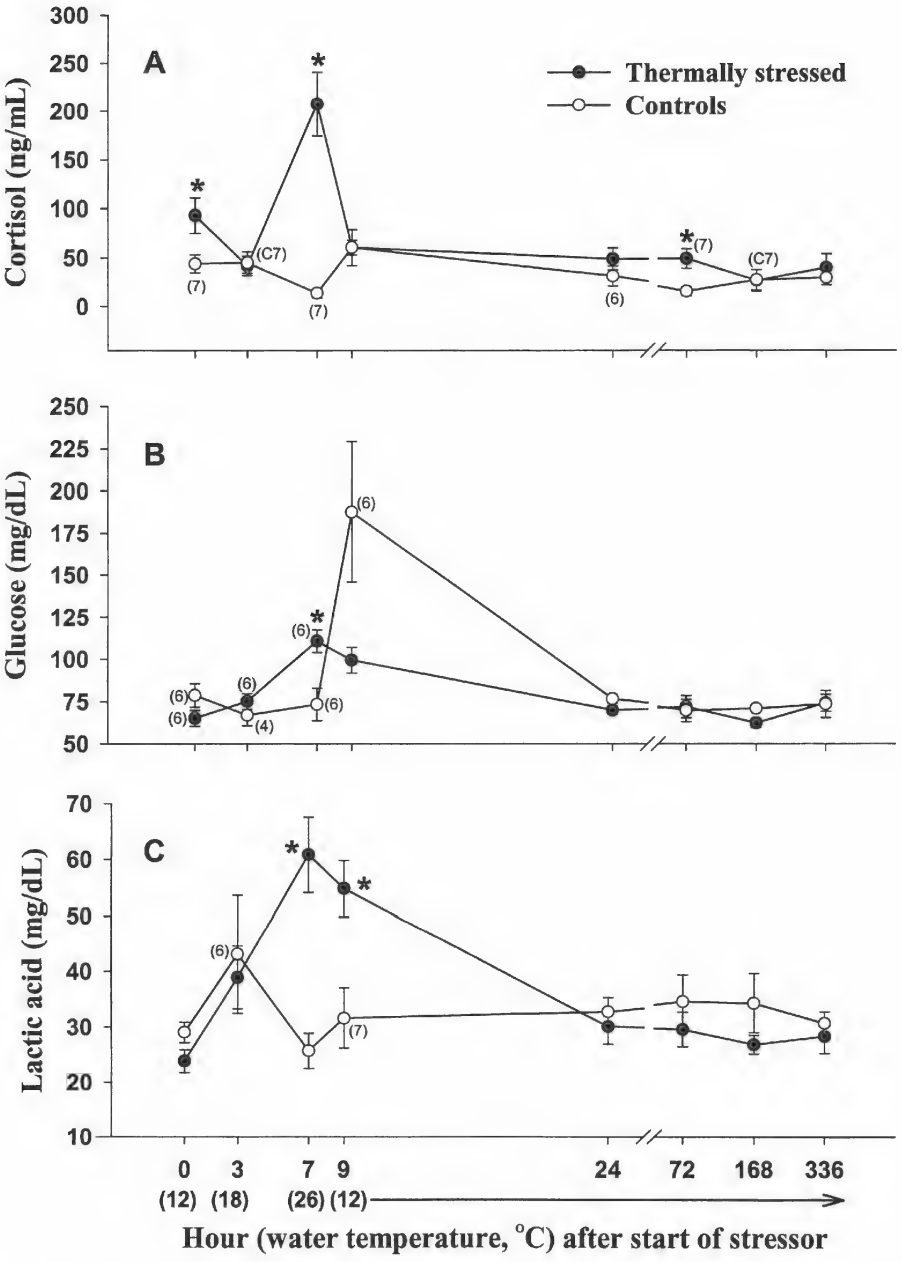

Figure 2. Mean (± SE) plasma (A) cortisol, (B) glucose, and (C) lactate concentrations for fish at selected time intervals after they had been exposed to Stressor 1 and for unstressed controls. Means were derived from eight fish unless otherwise noted parenthetically; C = control fish. An asterisk denotes a significant difference between treatment and control fish at that time interval.

lactate concentrations did not differ between treatment and control fish at any sample period from 24 hr on. Liver hsp70 content displayed a dramatic increase during the experiment that persisted for the entire two week period (Figure 3). Levels of hsp70 in treatment fish were significantly higher than control fish at all sample periods except the first two.

Discussion

Our results indicate that juvenile fall chinook salmon exposed to naturally-occurring thermal stress showed some physiological changes (Figure 2), a dramatic increase in levels of liver hsp70 (Figure 3), but no increase in vulnerability to predation and little direct mortality (Tables 1-3). These thermal stressors, which were derived from field data and included a 14°C temperature increase over several hours followed by a rapid decrease to ambient temperature, are unique stressors that, to our knowledge, have not been previously studied. Such thermal stress may be common in developed and highly managed river systems. Most research on thermal stress in fishes has focused on two broad areas: (1) examining the effects of acute temperature shocks, where fish acclimated to a certain temperature are subjected to dramatic changes in temperature usually within a few minutes (Coutant 1973, Wedemeyer 1973); and (2) examining the effects of different acclimation temperatures on selected measures of fish performance (Glova and McInerney 1977, Fuiman 1991, Cech et al. 1994). The wide variety of results produced by such studies indicates that they may not be useful for predicting the effects of acute thermal stressors, such as the types we evaluated, on fish. Indeed, the influence of thermal stressors on fish performance seems dependent on

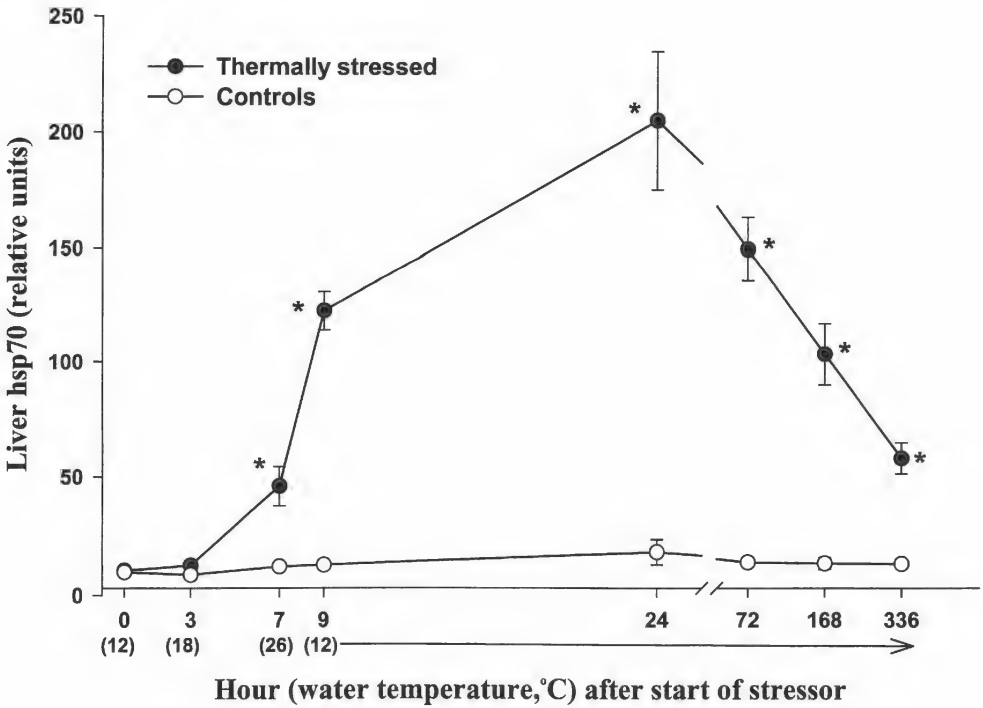

Figure 3. Mean (± SE; n = 8) liver hsp70 content for fish at selected time intervals after they had been exposed to Stressor 1 and for unstressed controls. An asterisk denotes a significant difference between treatment and control fish at that time interval.

numerous factors, including species, size and age, biology and physiology of the organism (e.g., eury- vs. stenothermal species), acclimation temperature, magnitude of temperature change, and tempering rate, among others.

Few juvenile fall chinook salmon died after exposure to our acute thermal stressors up to 26°C (i.e., Stressors 1 and 2), a temperature within the lethal range for this species (Brett 1952, Templeton and Coutant 1971). We attribute the lack of significant mortality in fish to the short time fish remained at 26°C and use of a slow tempering rate. Tempering rate influences the critical thermal maximum and survival of fish (Elliott and Elliott 1995, Clapp et al. 1997), and slow tempering may prolong the time of death (Mather and Wahl 1989). Although our tempering rates were much slower than most reported in the literature, they represent what these fish would experience in the wild and probably helped prolong the time of death. However, our results indicate that if fish remain at 26°C (i.e., Stressor 3) or are exposed to temperatures slightly above 26°C (i.e., Stressor 4), mortality quickly ensues. Thus, for fish in the wild, the presence and use of cooler water refugia may be critical to their survival. Our conclusion agrees with Mundahl (1990), who reported that survival of 14 fish species in shrinking stream pools depended on the use of cooler shaded refugia. Our results suggest that survival of fish trapped in pools may be high if they can tolerate periods of high temperatures until the pool re-floods with cool water.

Besides death, loss of equilibrium is a common response of fish to a sublethal exposure to lethal temperatures. In fact, only slight excursions of temperature above or below those normally encountered can elicit a sequence of behavioral and locomotory symptoms of sublethal thermal injury (Logue et al. 1995). Coutant (1969) argued that equilibrium loss is important for fish subjected to thermal stress because loss of equilibrium occurs sooner than direct mortality and may make fish particularly vulnerable to predation. Indeed, loss of equilibrium and aberrant behavior are often mentioned as probable causes of the increased vulnerability to predation of fish subjected to acute thermal shocks (Sylvester 1972, Coutant 1973). However, the acute thermal stress our fish received (i.e., Stressors 1 and 2) did not sufficiently compromise behavioral and performance factors that affect the vulnerability of prey fish to predation (Tables 1-3; Bams 1967, Coutant 1973, Mesa et al. 1994). Although we noted some aberrant behavior in fish as they approached the maximum temperature (e.g., erratic swimming or agitation), we saw no apparent behavioral differences in our treatment and control fish upon release to predators. Also, size of prey did not influence the outcome of our predation experiments. All fish responded to predation pressure by forming schools soon after attacks started. Thus, aside from species, age, or size differences, there appear to be differences in the nature and severity of acute thermal shocks and the type of thermal stress we exposed our fish to, at least with regard to predator avoidance ability. Juvenile fall chinook salmon were capable of avoiding predators soon after experiencing a thermal stressor of the type we used (Tables 1-3), a conclusion also noted in studies subjecting juvenile salmonids to physical stress (Olla and Davis 1989, Mesa 1994).

The physiological factors we examined indicated that exposure of our fall chinook salmon to an acute temperature increase was stressful. Plasma cortisol, glucose, and lactate all increased during the thermal warming, reached maximal values at the time of maximal temperature, and returned to levels similar to initial values by 24 hr (Figure 2). Some studies have reported similar responses, in terms of hypercortisolemia or hyperglycemia (or both), in other species exposed to thermal stress (Wedemeyer 1973, Strange et al. 1977, Kindle and Whitmore 1986, Thomas et al. 1986, Davis and Parker 1990). In contrast, some studies have shown little or no response of plasma cortisol and glucose in fish to thermal stress (Strange et al. 1977, Carmichael et al. 1984, Thomas et al. 1986). Thus, the physiological responses of fish to thermal stressors vary widely and may depend on species and type of stressor used. If plasma cortisol and glucose increase in response to thermal stress, they probably serve to mobilize energy stores for essential reactions (e.g., ATP production) and help maintain osmoregulatory function, among other things.

Plasma lactate concentrations were also higher in treatment fish relative to controls, significantly so at the time of maximum temperature and 1 hr after the cool down had occurred (Figure 2). We are unaware of other studies reporting changes in plasma lactate concentrations in fish subjected to thermal stress. Such elevations in plasma lactate indicate some degree of anaerobic metabo-

lism was occurring in fish exposed to the thermal stressor and are probably due to a combination of factors. During temperature increases in ectotherms, blood pH decreases and PCO_2 increases (Crawshaw 1979). At high temperatures and low pH, hemoglobin has a low affinity for oxygen (Schmidt-Nielsen 1991) and arterial PO_2 may decrease (Soncini and Glass 1997), thus leading to problems with oxygen delivery to the tissues. This, coupled with the increased metabolic demands and hyperactivity of our fish and the low oxygen carrying capacity of water at high temperatures, probably contributed to their lactacidosis. Such changes in the acid-base balance of fish subjected to temperature change probably contributes to mortality as lethal temperatures are approached.

Exposure of juvenile fall chinook salmon to Stressor 1 elicited a dramatic response in liver hsp70 content (Figure 3). The magnitude of maximum change represented a more than 25-fold increase over control levels. Mazur (1996) also reported that hsp70 levels in the gills of cutthroat trout were still elevated up to 3 wk after fish were exposed to a 2 hr, 15°C heat shock (7.4-22.4°C). Heat shock proteins (hsps) are a group of proteins synthesized by cells in response to heat and many other types of stressors, such as exposure to contaminants (Lindquist 1986, Lindquist and Craig 1988, Iwama et al. 1998). The constitutive and inducible expression of hsps is perhaps the most highly conserved genetic system known, existing in all organisms from bacteria to plants and animals. The functions of hsps in response to stress help to maintain cellular homeostasis and include protein assembly, correct folding and translocation, and regulating hormone-receptor interactions (Iwama et al. 1998). The hsps prevent the aggregation and facilitate the renaturation of heat-damaged proteins following a heat shock, thus they play a vital role in thermotolerance (Tomanek and Somero 1999). In short, the hsp70 response of our fish probably provided cellular protection and enhanced survival against a thermal insult that approached the upper lethal temperature limits for this species.

In summary, we have shown that exposure of juvenile fall chinook salmon to naturally occurring thermal stressors elicited some acute physiological stress responses and a significant and prolonged elevation of liver hsp70 content, but did not lead to substantial mortality or increased vulnerability to predation. The physiological changes seen in our fish, and the consequences of exposing fish to multiple stressors, should be of concern to those charged with management of the Hanford Reach area.

Acknowledgements

We thank our colleagues at the Columbia River Research Laboratory and the WDFW Kennewick Field Office for their assistance in the laboratory and field; Jack Hotchkiss for conducting the cortisol assay; and Paige Ackerman for helping us set up the hsp70 assay.

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Received 18 June 2001
Accepted for publication 30 December 2001

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Roman Biek,[1] Naturschutz II, Fachbereich Biologie, Philipps Universität Marburg, 35037 Marburg, Germany,

L. Scott Mills, Wildlife Biology Program, School of Forestry, University of Montana, Missoula, Montana 59812,

and

R. Bruce Bury, USGS Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331

Terrestrial and Stream Amphibians across Clearcut-Forest Interfaces in the Siskiyou Mountains, Oregon

Abstract

Timber harvest in the Pacific Northwest has resulted in a highly fragmented landscape, but there is no information on responses of amphibians to forest edges for this region. We investigated abundance of terrestrial and stream-dwelling amphibians on the interface of recent clearcuts and mature forest in the Siskiyou Mountains, Oregon, in summer and fall of 1998. We assessed relative abundance of terrestrial amphibians on four clearcut-forest transects with a combination of pitfall trapping and manual searches. Ensatinas and Del Norte salamanders, the most frequently recorded species, were found on all four sites. While we commonly captured ensatinas using both techniques, we caught most Del Norte salamanders during manual searches. For both species we found no differences in abundance associated with distance to forest edge. Lack of differences in salamander abundance among clearcut and adjacent forests may be related to large amounts of small woody debris that remained in the clearcuts. The abundance of larvae of tailed frogs and Pacific giant salamanders in five headwater streams was markedly lower in clearcuts than in downstream mature forest stands. No obvious differences existed for stream habitat variables across transects, but abundance of metamorphosed individuals and recruitment may be reduced in clearcut areas due to hotter and drier conditions during the summer.

Introduction

Next to loss of forest habitat, the increasing proportion of edges is considered one of the most problematic consequences of forest fragmentation (Murcia 1995). Because forests abutting harvested areas are subject to changes in physical and biotic conditions, forest species may have reduced abundances or be excluded from edge habitats (Mills 1995, Jules 1998). This is especially true for species susceptible to the drier, warmer conditions typical of deforested areas and forest edges (Murcia 1995). Because of their ectothermal lifestyle and often low tolerance to high temperatures and water loss (Stebbins and Cohen 1995), many amphibians are negatively affected by timber harvest (deMaynadier and Hunter 1995).

In the Pacific Northwest, extensive timber harvest has occurred over the last 100 yr. Only about 17% of the pre-settlement coniferous forest has not been logged (Spies and Franklin 1988), resulting in a high proportion of early-successional forest. Certain amphibian species in the region are associated with habitat conditions realized primarily in old-growth stands (Welsh 1990, Ruggiero et al. 1991). However, it is unknown whether increasing amounts of forest edges might further reduce the abundance and distribution of those species. While recent studies in the eastern United States have demonstrated that some amphibians are negatively affected by forest edges over relatively short distances (deMaynadier and Hunter 1998, Gibbs 1998) we are unaware of any published studies on the topic in the Pacific Northwest. Also, little is known about the effects of fragmentation and edge on stream amphibians. Although forest harvesting has negative impacts on many stream amphibians (Bury and Corn 1988, Corn and Bury 1989), it is unclear whether those impacts are limited to the harvested area itself or if they would also influence downstream areas.

We investigated the distribution of amphibians across clearcut-forest interfaces in the Siskiyou Mountains, Oregon, a region with a diverse and unique herpetofauna (Bury and Pearl 1999) and

[1]Author to whom correspondence should be addressed. Current address: Wildlife Biology Program, School of Forestry, University of Montana, Missoula, Montana 59812
E-mail: rbiek@selway.umt.edu

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high levels of forest fragmentation (Jules et al. 1999). Our objectives were to compare the presence and abundance of terrestrial and steam amphibians in transects across recent clearcuts, the interface of forest edge, and late-successional forests.

Methods

Study sites were in the Siskiyou National Forest, located in the central part of the Siskiyou Mountains, southwestern Oregon (Figure 1). The climate in this area is Mediterranean with hot, dry summers and cool, moist winters. Almost all precipitation falls from October to May. Below about 1200 m, Douglas-fir (*Pseudotsuga menziesii*) and occasionally sugar pine (*Pinus lambertiana*) dominate the upper canopy. A lower canopy is formed by evergreen hardwoods such as tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), chinquapin (*Castanopsis chrysophylla*), and canyon live oak (*Quercus chrysolepis*). At higher elevations (>1200 m), hardwoods are scarce or absent and Douglas-fir is replaced by true firs (*Abies* spp.). At all but the highest elevations, Port Orford cedar (*Chamaecyparis lawsoniana*) and bigleaf maple (*Acer macrophyllum*) are found at sites with continual water supply, such as near springs and small streams (Whittaker 1960).

Terrestrial Sites

We maximized edge contrast by choosing four stands of uncut forest >180 yr old adjacent to clearcuts <15 yr old (Table 1, Figure 1). To fit several sampling plots and to provide a 50 m buffer from roads and streams, edges had to be at least 250 m long and relatively straight. Southern, drier aspects were not sampled. These constraints and the need for a daily site check during pitfall trapping precluded random site selection.

All four uncut forest sites were at least 13 ha (Table 1). This size was considered sufficient to

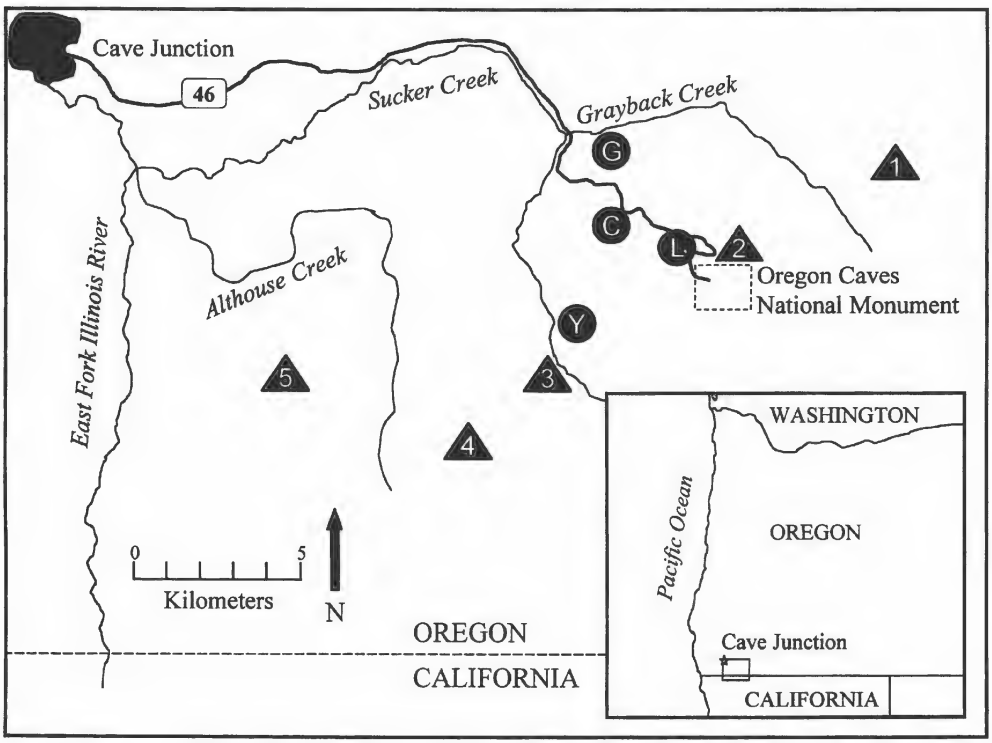

Figure 1. Study area in Siskiyou National Forest, southwestern Oregon showing locations of terrestrial (●) and aquatic (▲) study sites.

TABLE 1. Characteristics of forest stands and adjacent clearcuts surveyed for terrestrial amphibians on forest edges in Siskiyou National Forest, Oregon. Elevation was measured at approximate midpoint of surveyed length of edge.

Site	Age (yr)	Size (ha)	Elevation (m)	Slope (%)	Aspect	Bearing of edge	Size of cut (ha)	Year cut
L	>200	60	1020	50	N	ESE	5	1986
G	>200	34	810	46	NNE	SE	26	1986
C	>300	13	960	43	NE	SE	13	1986
Y	>180	21	960	31	W	S	6	1990

provide areas uncompromised by edges, based on a depth of influence of 25–65 m in previous work on forest amphibians in the eastern United States (DeGraaf and Yamasaki 1992, deMaynadier and Hunter 1998) and studies on small mammals and herbaceous species in the Siskiyou Mountains (Mills 1995, Jules 1998). After logging, all clearcuts had been burned and planted with Douglas-fir seedlings. Also, to reduce competition with the conifers, young hardwoods had been cut down repeatedly, resulting in large amounts of slash and small logs on the ground in the harvested stands.

At each site, we installed 15 pitfall traps, arranged in five parallel lines each containing three traps spaced 25 m apart. Lines were placed in the clearcut at 15 m and 45 m from the edge, and at 15 m, 45 m, and 75 m in the forest (Figure 2). Each trap was built from two number 10 tin cans taped together for a deep trap and included a plastic funnel (Corn and Bury 1990). We also added three drift fences pointing away from each trap in 120-degree angles (modified from Corn and Bury 1990) made of transparent polyethylene supported by wooden stakes. Fences were 3 m long and ~30 cm tall after being buried 10 cm deep in the ground. We opened traps for 61 consecutive days from 1 October to 1 December 1998. We checked traps daily in the early morning during times of high capture probability (immediately after trap opening and after rainfall) and every other day for the remaining time. We recorded species, sex, snout-vent length, and total length (both to the nearest mm) for every capture. The second toe on the left hind foot was clipped to recognize recaptures. We released animals immediately at about 5 m from the trap next to a cover object.

We also manually searched for amphibians on plots that were 50 m long (parallel to the edge) and 30 m wide. Plots were directly adjacent to each other to form a transect running from 60 m into the cut to 90 m into the forest interior. We sampled two such plot transects at each edge site (Figure 2). We avoided patches that were structurally different (e.g. small wind throws), so that pitfalls grids and search transects were placed at variable distances from each other (5-500 m). Searching for amphibians combined time- and area-constrained sampling (Corn and Bury 1990). Four persons systematically searched through each 50 x 30 m plot for 1 hr (4 person hr). Starting at the downhill end of the plot, searchers moved uphill while turning all moveable cover objects including rocks, small logs, and pieces of bark on the ground. Well-decayed logs and the space between bark and log surface were also probed or separated. We spent ≤10 min searching any log to ensure an even distribution of search efforts (Corn and Bury 1990). We sampled all five plots in one transect in the same day. We searched sites twice on four consecutive days (18-21 and 25-28 November 1998) during wet and non-freezing conditions. We pooled numbers of animals found during both sampling sessions for each site.

Using line intersect sampling (DeVries 1974), we determined the amount of downed wood within each edge class, employing two 20-m line-intercept transects with random orientation with the midpoint of each line equidistant from two pitfall traps (Figure 2). For every log intersecting the line, we recorded length, diameter at both ends and the middle, type (hardwood or conifer), and degree of decay on a scale from 1 (mostly intact) to 3 (mostly decayed). Definition of a log followed Mills (1995) who included any dead woody material closer than 45° to the ground that was greater than 10 cm diameter at the larger end. Log volume (m^3/ha) and log density (number/ha) were estimated based on the 40 m of total transect in each edge class (DeVries 1974, Mills 1995).

We measured temporal changes of topsoil moisture across the surveyed forest edges in June, July, August and October 1998, sampling three of the sites (all except Y) once a month, after at least 48 hr without rainfall. Sampling followed a

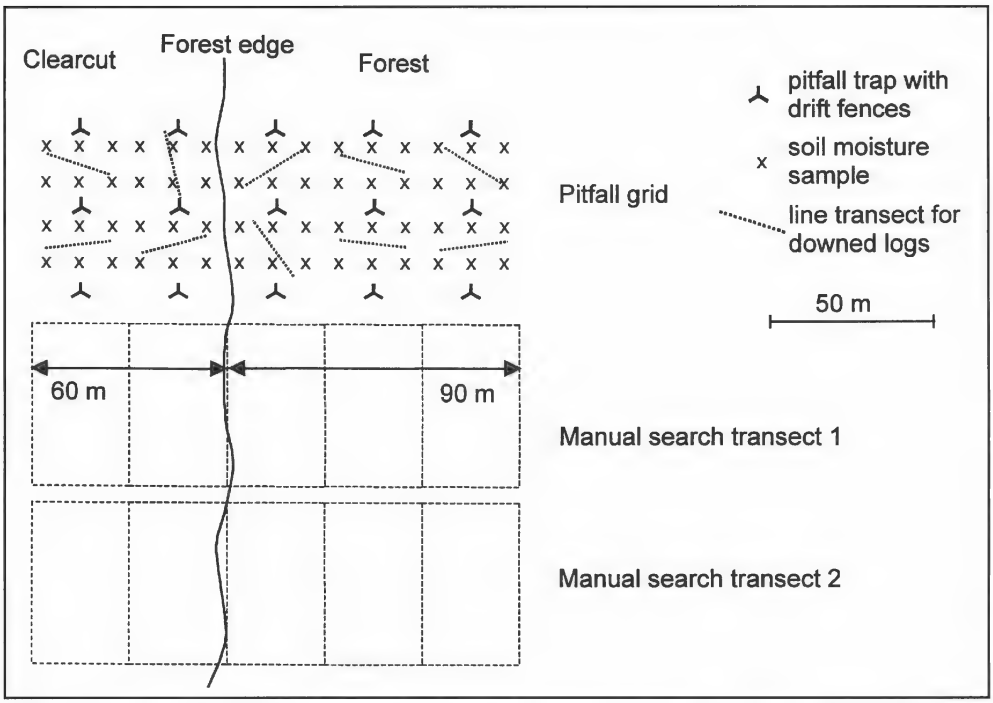

Figure 2. Schematic view of forest edges and spatial application of sampling procedures used. Distances between pitfall grid and manual search transects varied from site to site and are not shown to the actual scale.

systematic design with 12 soil samples spaced ca.10 m apart within each edge class (= 60 samples per site and month). The exact sampling spot was determined by throwing a shovel over a shoulder. Each soil sample (32 cm^3) was placed in a plastic container after removing visible rocks and coarse organic matter, and taken to the lab to be oven dried for 48 hr at 95° C. The difference between dry and fresh weight divided by the volume gave percent water content.

Stream Sites

To investigate the effects of forest edges on stream amphibians, we selected five headwater streams flowing from clearcuts into uncut stands of older forest (Figure 1). While specific estimates for forest age were not available, all stands represented late-successional forest. The adjacent stands had been clearcut 26-34 yr ago. Regeneration appeared to be slow and trees planted in the cut did not exceed 5 m in height. We chose only permanent first and second order headwater streams that had sufficient water flow during the dry summer months to support stream amphibians. Average stream width varied from 1.1-2.0 m and elevation of the sites (as measured on the clearcut-forest boundary) was 750-1230 m. The streams lacked a buffer zone separating them from the clearcut area, but were usually shaded by small trees, mainly willows and alders (2-5 m high).

We defined the edge for streams as the straight line perpendicular to the stream that connected the two outermost mature trees (dbh >25 cm) of the forest within 15-50 m on each side of the stream channel. Trees closer than 15 m were excluded because some single trees close to the stream had been spared from logging. These trees would have put the edge far into the clearcut. Roads and forest of various ages were upstream of all clearcuts. At each site, we established five 5-m long sampling segments at the edge (0 m), and at 50 m and 100 m into clearcut and forest. If sampling segments were at unusual locations such as waterfalls or piles of logs, we moved sampling

segments ± 5 m away from the feature. We recorded general data on stream variables in July and August prior to the amphibian sampling. For every 1 m section of each 5 m segment we measured stream width and dominant substrate, and scored pool ratio based on a scale from 1 to 10 (Bury and Corn 1991). We estimated embeddedness of rocky substrate (>65 mm) with fine sediment on a scale from 1 (less than 20% covered) to 5 (at least 80% covered). For each segment, we recorded gradient of the stream and both side slopes and measured stream temperature.

Amphibian sampling followed the protocol of (Bury and Corn 1991) and occurred 23 July-15 August 1998 when weather conditions were hot and dry. A drift net (window screen, 2 mm mesh) was installed at the downstream end of the segment. We searched each segment in 1-m intervals, first by turning over rocks on the stream bank up to 50 cm away from the stream and then by searching the stream. We sampled by turning all moveable rocks and woody materials, removing them from the stream and placing them on the stream bank. A dip net or piece of hardware cloth was placed immediately downstream. Also, we frequently checked the drift net at the downstream end for dislodged animals. After sampling the 5-m area, we replaced cover and released all animals into the stream. We sampled all five segments per site consecutively starting from the downstream end (+100 m), and finished within 2-3 days. Captures are expressed as numbers per m^2 based on the measured widths for the sampled segments.

Data Analysis

Using an ANOVA procedure we tested the null hypothesis that biotic and abiotic variables (grouped in edge classes) remained constant across edges. Edge distance was thereby treated as a fixed main factor. Whenever the assumption of homogeneous variances was met, a two-way ANOVA was performed that added 'site' as a random factor for blocking (Sokal and Rohlf 1981). Otherwise, data were square root transformed {square root (x) + square root (x+1)}. If transformations failed to correct the problem, a one-way ANOVA robust to unequal variances (Rice 1989) was used instead. Due to the inability to block for site in this alternative procedure, the power to detect differences associated with edge distance declined considerably. We refer to the resulting *P*-values of either test as $P_{distance}$.

Next, we asked whether differences between edge classes occurred at random or if they had a directional component in being ordered in a consistent fashion. The ordered heterogeneity test (Rice and Gaines 1994) specifically addresses this aspect of directionality and has been successfully applied in previous edge studies (Mills 1995). In this procedure, the result of a heterogeneity test (e.g., an ANOVA *P*-value) is combined with an order component (rank correlation) to calculate a final *P*-value. We computed Spearman's rank correlation between edge distance and means for this purpose and used the $P_{distance}$ value calculated in the ANOVAs described above. Results from the ordered heterogeneity test are designated as P_{edge}.

To account for the inflated Type I error arising from testing the same alternative hypothesis (edge trend) repeatedly, we performed a sequential Bonferroni correction (Rice 1989) of *P*-values for each group of tests (terrestrial salamanders, soil moisture levels, coarse woody debris, stream variables, and stream amphibians). We considered a probability level of ≤0.05 as significant.

Results

Terrestrial Forest Edges

We captured 98 individuals of six amphibian species in pitfall traps (Table 2). Numbers varied among sites from 9 to 37 captures. Ensatina (*Ensatina eschscholtzii*) was the most common species, representing 75% of all captures. Ensatina and Del Norte salamander (*Plethodon elongatus*) were the only species caught at all four sites. All other amphibian species were caught in low numbers (<10) at between one and three of the sites (Table 2).

In 160 person hours of manual search, we caught 165 amphibians of which most (99%) were plethodontid salamanders (Table 2). Ensatina was the most common species found with this technique; 80% of captures were in or under logs. We also frequently found Del Norte salamanders, predominantly beneath rocky substrate (60%) and to a lesser degree under logs or bark on the ground (30%). Both species were detected at all four sites. We captured 7 of 12 clouded salamanders (*Aneides ferreus*) near the forest edge, mainly in association with logs.

TABLE 2. Mean amphibian captures (± SE) using live pitfall trapping and hand collection across four forest edges at Siskiyou National Forest, Oregon, fall 1998. N = total number of individual captures. Edge distance refers to the perpendicular distances from the edge into clearcut (negative values) or forest (positive values).

Species	Sampling	N	Sites	Edge distance (m) -45	-15	+15	+45	+75	$P_{distance}$[a]	Rank[b]	P_{edge}[c]
Pacific giant salamander	Pitfall	8	3	0.0 (0.0)	0.3 (0.3)	0.3 (0.3)	0.5 (0.3)	1.0 (0.7)	–	–	–
	Search	–	–	–	–	–	–	–	–	–	–
Ensatina	Pitfall	70	4	4.5 (1.3)	5.8 (2.1)	2.5 (0.6)	1.5 (1.0)	3.3 (1.3)	0.041	-0.60	0.102
	Search	90	4	2.8 (0.6)	3.5 (0.8)	4.0 (0.8)	7.3 (2.8)	5.0 (1.7)	0.921[d]	0.90	0.284
Del Norte salamander	Pitfall	8	4	0.3 (0.3)	0.5 (0.3)	0.8 (0.3)	0.3 (0.3)	0.3 (0.3)	–	–	–
	Search	62	4	3.0 (2.0)	4.5 (1.6)	3.5 (1.8)	2.3 (1.0)	2.3 (1.0)	0.578	-0.67	0.348
Clouded salamander	Pitfall	1	1	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	–	–	–
	Search	12	3	0.3 (0.2)	0.8 (0.4)	1.0 (0.5)	0.8 (0.4)	0.3 (0.2)	–	–	–
Rough-skinned newt	Pitfall	5	2	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	–	–	–
	Search	–	–	–	–	–	–	–			
Tailed frog	Pitfall	6	2	0.3 (0.3)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	1.0 (0.6)	–	–	–
	Search	1	1	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	–	–	–

[a]Two-way ANOVA testing for main effect of edge distance while using site as a blocking term.

[b]Spearman's rank coefficient for mean captures relative to edge distance.

[c]Ordered heterogeneity test (Rice and Gaines 1994) after sequential Bonferroni correction for multiple tests (Rice 1989).

[d]One-way ANOVA robust to heterogeneous variances used with edge distance as the only explanatory variable

The proportion of adult (>50 mm) to juvenile ensatinas caught in pitfalls (73: 27) was higher than found with manual searches (40:60). Searches also yielded fewer adult than immature Del Norte salamanders (40:60); pitfall captures were too low for such a comparison in this species. Age proportions among edge classes did not differ significantly for ensatinas in pitfalls ($P = 0.980$) or manual searches ($P = 0.209$), nor for Del Norte salamanders in manual searches ($P = 0.240$).

Owing to small sample sizes for most species, tests for an edge trend were only performed for ensatinas (data from pitfalls and manual searches) and for Del Norte salamanders (manual searches only). None of those tests identified a significant trend in relative abundance across the clearcut-forest gradient (Table 2). Notably, the higher number of ensatinas caught in pitfalls in clearcuts suggested a trend opposite to that based on manual searches, during which ensatinas were more commonly found in the forest.

Quantities of downed wood were significantly greater in the clearcut compared to the forest for both volume ($P = 0.026$) and density of logs ($P = 0.014$) (Figure 3). Specifically, several hundred cubic meters per hectare were estimated for the logged area compared to ~100 m^3 in the forest. We also noted a marked contrast for number of logs with 2000-3000 per ha in clearcuts and ~200 per ha at 75 m into the forest. Within the forest, areas closer to the edge had more logs on the ground compared to the forest interior, but volume of downed wood was uniform across the same spatial scale. The vast majority of logs on all sites comprised moderately decayed hardwoods.

Soil water content in June was relatively uniform across the clearcut-forest transect with values ranging around 35%. Then, moisture diminished quickly and average water content fell to 17-21% in July and 10-15% in August. In summer, values generally were lower in clearcuts than in the forest. In late October, after the onset of autumn rainfall, this trend was reversed and water content was >38% in the clearcut compared to ~30% in the forest. While differences among edge classes were pronounced in July, August, and October, there was no significant directional trend across edge classes after correcting for multiple testing (all $P = 0.080$).

Stream Sites

We found two species of stream amphibians at all sites. Densities of tailed frog tadpoles (*Ascaphus truei*) were generally higher within forests including the edge compared to clearcuts (Figure 4). Adult and subadult frogs were uncommon and differences in numbers were less pronounced across edges. A high level of variation in tadpole densities across sites was caused by rarity of tadpoles in one of the streams.

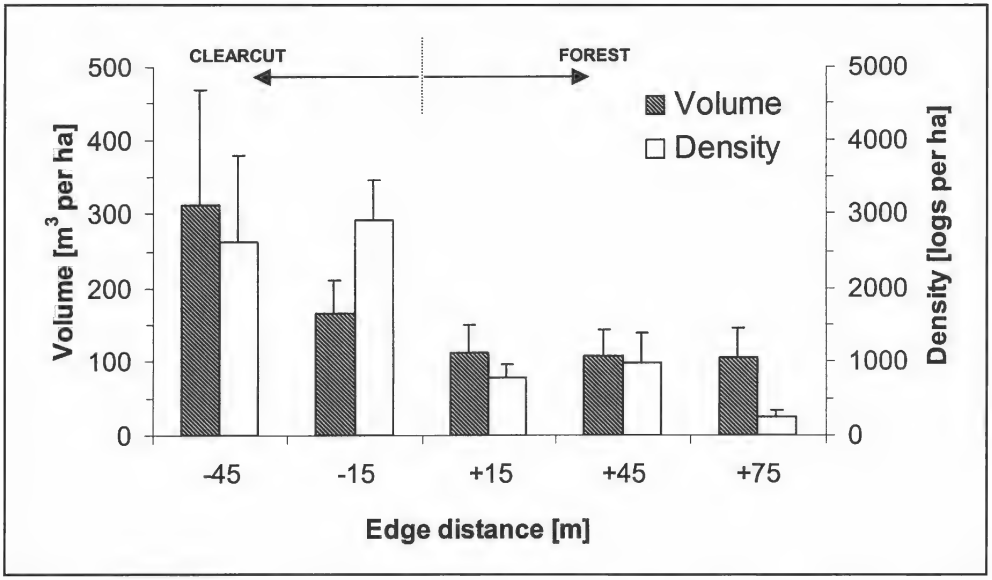

Figure 3. Estimated means (± SE) of density and volume of coarse woody debris across four clearcut-forest gradients, Siskiyou National Forest, Oregon, 1998.

Although Pacific giant salamander (*Dicamptodon tenebrosus*) larvae were more common in clearcuts than were tailed frog larvae, their densities also increased toward the forest interior (Figure 4). There was a significant negative trend from forest to clearcut for tailed frogs ($P = 0.022$) and nearly so for Pacific giant salamanders ($P = 0.054$).

We also encountered 32 metamorphosed tailed frogs during the searches (26 adults, 6 juveniles). Numbers per m^2 averaged 0.11 in the clearcut, 0.18 for the edge, and 0.21 for the forest interior (Figure 4). Because sample size was small and we are unsure whether the proportion of the frogs hiding in the stream remained constant across the edge transect, we did not subject these data to a test of edge trend.

No significant differences in gradient (percent drop), dominant substrate, pool ratio, embeddedness with fine sediment, water temperature, side slope, or canopy cover were found among the segments sampled within streams (Table 3). Canopy cover was highly variable in clearcuts, ranging from 28% to 95%, and no significant differences in canopy cover were found overall among edge classes. This was because along some streams small trees in the clearcut area provided shading.

Discussion

Terrestrial Sites

We obtained sample sizes sufficient for analysis for only two species of woodland salamanders. Members of this group are considered sensitive to the effects of timber harvesting (deMaynadier and Hunter 1995, Welsh and Droege 2001).

Ensatina is a widespread salamander in the Pacific Northwest, occupying a variety of forest habitats (Nussbaum et al. 1983). It occurs in oak woodland in California and, in the Pacific Northwest, reaches highest abundances in dry old-growth stands (Aubry and Hall 1991, Welsh and Lind 1991). Thus, it may have a relatively higher tolerance to high temperatures and low moisture compared to other western salamanders. Although usually not considered a species threatened by forest harvesting, positive associations with stand age were suggested for ensatinas in some areas (Raphael 1988, Welsh and Lind 1991, Aubry 2000).

Many studies suggest that structural features rather than stand age might influence the local abundance of woodland salamanders. Ensatinas, specifically, appear to have strong associations

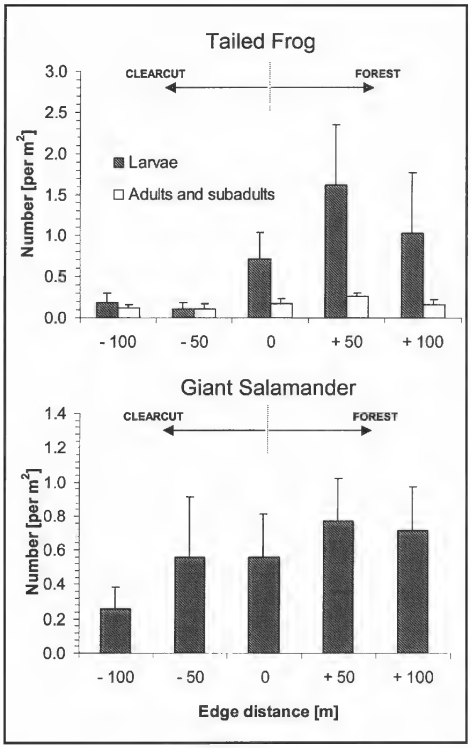

Figure 4. Densities (± SE) of tailed frogs and Pacific giant salamanders in five headwater streams flowing from clearcuts into downstream mature or old-growth forest in the Siskiyou National Forest, Oregon, 1998.

with woody debris (Butts and McComb 2000), including small logs (Welsh and Lind 1991). Volume and density of decaying logs were much higher in clearcuts than in adjacent forests (Figure 3), as a result of cutting undesired hardwoods in regenerating Douglas-fir stands. These large amounts of downed wood may be a beneficial habitat feature for ensatinas in clearcuts by providing shade and cover. This may allow the ensatina in the Siskiyous to inhabit forest edges and harvested stands to a similar level as contiguous forest.

Most ensatina captures in pitfalls occurred in clearcuts whereas capture rates were higher inside the forest during manual searches (Table 2). Our monitoring of soil moisture content indicated that the forested portion of the edge transect received less precipitation after the onset of rainfall in October than the adjacent clearcut, clearly a result of the intercepting canopy cover in forests. Thus, pitfall captures may have been higher in the clearcut due to microclimatic conditions there permitting surface activity earlier than in the forest.

The Del Norte salamander is endemic to the Siskiyou region (Nussbaum et al. 1983). Rocky substrates are an important habitat prerequisite for its occurrence (Herrington 1988, Welsh and Lind 1995) and its highest densities are usually found in old-growth stands (Raphael 1988, Welsh 1990, Welsh and Lind 1991, 1995). In contrast, Diller and Wallace (1994) found no correlation between Del Norte salamander occurrence and

TABLE 3. Habitat variables measured in five streams at same edge distances sampled for amphibians. Shown are means (± SE). Differences between means were tested with two-way ANOVA (except where indicated) with site as block and site by edge distance as error terms. *P*-values shown are corrected for multiple testing of the hypothesis of edge differences. Proportions were arcsine transformed prior to analysis.

	Edge distance (m)					
	-100	-50	0	+50	+100	*P*
Stream gradient (%)	11.0 (0.8)	11.0 (1.6)	15.8 (5.5)	9.2 (1.2)	8.0 (1.1)	0.826
Dominant substrate[a]	8.6 (0.5)	8.8 (0.4)	9.0 (0.2)	8.6 (0.2)	8.8 (0.1)	0.971
Pool ratio[b]	4.3 (0.5)	4.8 (0.4)	3.4 (0.3)	3.7 (0.5)	4.7 (0.4)	0.378
Embeddedness[c]	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	–
Side slope	39.0 (3.6)	39.9 (7.6)	36.6 (3.8)	39.0(5.5)	36.4 (1.8)	0.980
Water temperature (°C)	15.0 (1.3)	14.6 (1.1)	14.3 (1.0)	14.4 (1.0)	14.3 (0.7)	0.837
Canopy cover (%)	59 (13)	69 (12)	76 (6)	86 (3)	84 (3)	0.680[d]

[a]Mean size of dominant substrate on scale from 1 (silt/clay) to 10 (> 256 mm)
[b]Proportion covered by pools on scale from 1 (all riffle) to 10 (all pool)
[c]Degree of sedimentation with fine substrates on a scale from 1 (<20%) to 5 (>80%)
[d]One-way ANOVA used due to heterogeneous variances

forest age or canopy cover in a marine-influenced, moister study area located closer to the coast. These data suggest that in inland regions, Del Norte salamanders could likely be affected by clearcuts and forest edges. However, we found no differences in relative abundance among clearcut, forest edge, and forest interior for this species. Like ensatinas, we suggest that large amounts of woody debris maintain tolerable conditions for the Del Norte salamander in clearcuts. We caution, however, that our inference is limited to one year of data collected at few sites on north- and west-facing slopes. We are unable to draw conclusions about edge effects at other aspects. Also, we cannot rule out that edge effects reach even farther into the forest than the 90 m we sampled, as has been found for several abiotic variables (Chen et al. 1995). Finally, Del Norte salamanders were not abundant on any of our four sites, based on an average of 0.4 individuals found per person hour of search. This number is low compared to >4 salamanders per person hour found in some mature forests (Welsh and Droege 2001).

We also found constant proportions of adult and immature ensatinas and Del Norte salamanders across edge classes, showing that location relative to the edge did not affect population structure in either species. Similarly, Grialou et al. (2000) reported equivalent size distributions of ensatinas in clearcuts and adjacent forests.

Although limited in scope, our study suggests that terrestrial salamanders in the Siskiyou Mountains were not negatively affected by forest edges on northern and western slopes and for distances up to 90 m into the forest interior. This may also mean that smaller clearcuts with such exposure do not represent dispersal barriers for those species.

Stream Sites

We found a difference of larval densities across the clearcut-forest interface for both species of stream-dwelling amphibians with lowest numbers at the farthest distance into the clearcut area. Tailed frogs depend on cool, fast-flowing streams, and are sensitive to impacts of timber harvest (Bury and Corn 1988, Dupuis and Steventon 1999). In southwest Oregon and northwest California, 81% of streams flowing through old-growth forests had tadpoles compared to only 11% of streams in young stands (Welsh 1990). However, Diller and Wallace (1999) reported that tailed frog populations in the milder Californian coastal belt were associated with substrate parameters and gradient rather than forest age or canopy closure.

Association with forest age is less clear for Pacific giant salamanders. Adults are equally common in naturally regenerated forests of young, mature, and old age (Corn and Bury 1991, Welsh and Lind 1991). Larval densities also did not differ with forest age in unmanaged uncut forest (Bury et al. 1991), but were reduced in logged areas compared to uncut forest and especially in low gradient streams (Corn and Bury 1989). In contrast, two studies reported higher salamander densities or biomass after logging, probably due to a temporary increase in productivity and prey base (Murphy and Hall 1981, Hawkins et al. 1983).

We found that larval densities decreased with increasing distance from the downstream forest. Since stream habitat and temperature were not appreciably different across the 200 m clearcut-forest transect, other factors are likely responsible for these differences. We suggest that the observed patterns could be explained by the terrestrial habitat requirements of Pacific giant salamanders and tailed frogs. Metamorphosed Pacific giant salamanders appear to depend on cool and moist conditions (Welsh and Lind 1991, Gomez and Anthony 1996), and immediate responses of terrestrial adults and juveniles to clearcutting may be negative (Cole et al. 1997). Abundance of larvae also increases with the amount of large woody debris available close to the stream, possibly because such logs provide important cover for adults (Wilkins and Peterson 2000). Also, adult tailed frogs have low tolerance to dry conditions and high temperatures (Claussen 1973a,b). These data suggest that clearcuts may provide unsuitable habitat for the terrestrial stages of both Pacific giant salamander and tailed frog. Consequently, a locally lower density of adults would reduce recruitment and larval densities of streams flowing through clearcuts.

The suggested explanation would imply that movement of amphibians from forest into the upstream clearcut during reproduction is limited. Indeed, extreme philopatry is typical for the tailed frog and only immature frogs disperse over several hundred meters (Daugherty and Sheldon 1982). Aubry (2000) caught few juvenile and adult tailed frogs in managed forests compared to unmanaged stands, and he suspected that local extinctions from

streams in harvested stands may be related to restricted movements of frogs through managed upland habitat. Our results for stream amphibian captures in pitfall traps were consistent with the hypothesis of higher abundance under closed canopies since the majority of tailed frog and Pacific giant salamander captures occurred in the forest interior (Table 2).

Dispersing tailed frogs and Pacific giant salamanders may be able to traverse clearcuts during environmentally favorable conditions. However, some data from the eastern U.S. suggest that forest edges may limit movements of dispersing amphibians (Gibbs 1998) and that especially newly metamorphosed individuals prefer closed canopy situations (deMaynadier and Hunter 1999). The question of which factors contribute to successful dispersal and colonization of amphibians in the Pacific Northwest deserves particular attention by wildlife research and management.

Effects of future harvesting on larvae of stream amphibians may be a lesser problem because riparian buffers are now being left along many Northwest streams. Such buffers appear to be effective in mitigating the effects of harvesting on stream amphibians in British Columbia (Dupuis and Steventon 1999), but are less well studied farther south. Still, new regulations are primarily intended to maintain conditions within the stream and on the stream bank. Whether such buffer zones will also provide sufficient habitat for the terrestrial life stages of stream amphibians is unclear. For stream amphibians in the Pacific Northwest, edge effects may be of concern, especially in landscape situations where forested buffer strips are still lacking or where local recolonization will depend on movement through harvested upland habitats.

Acknowledgements

We are grateful to many people at the Oregon Caves National Monument, particularly John Roth and Roger Brandt, and to the U.S. Forest Service for assistance and important information. We thank Kelly Droege, Sandra Hüttenbügel, Andrea Kortello, Laurie Nicholson, Ron Reed, and Eric Unger for field assistance. Dave Tallmon and an anonymous reviewer gave helpful comments on earlier drafts. Roman Biek thanks Peter Poschlod for his encouragement throughout the study. The research was supported by USDA Competitive Grant 97-35101-4355, NSF MONTS 291835 and NSF DEB-9870654 to L. S. Mills, and partial support from the DOI/USDA Joint Fire Science Program to R. B. Bury.

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Received 14 June 2001
Accepted for publication 15 November 2001

Evelyn L. Bull,[1] USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97859

and

Mark P. Hayes, Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501

Overwintering of Columbia Spotted Frogs in Northeastern Oregon

Abstract

We studied behavior and locations of overwintering Columbia spotted frogs in northeastern Oregon. We monitored 66 radio-tagged frogs as they moved to overwintering sites during 1997-2000. Frogs used a diversity of overwintering sites, but all sites had an aquatic component including ice-covered ponds (44%), partially-frozen ponds (29%), lotic habitats (23%), and temporary backwaters and seeps (4%). The distance between the original point of frog capture in August-September and the overwintering site varied from 15 to 1200 m. Individuals in ponds were active all winter and remained in shallow water within 1 m of the shore. Frogs overwintering in ponds selected microhabitats with significantly higher water temperatures and dissolved oxygen concentrations compared to other locations in the ponds. Movements during the overwintering period appeared to be linked to water temperatures and dissolved oxygen concentrations.

Introduction

Knowledge of overwintering sites is one of the major gaps in our understanding of ranid frog ecology. Authors have speculated about overwintering habitats (Nussbaum et al. 1983), but precise overwintering locations are known for few species. Temperate marsh- and pond-dwelling ranid frogs often overwinter underwater, although some of the same species have been observed overwintering terrestrially at lower elevations. Overwintering sites have been described for the common frog (*Rana temporaria*) (Smith 1951, Koskela and Pasanen 1974), pickerel frog (*R. palustris*) (Logier 1952, Johnson 1987), leopard frog (*R. pipiens*) (Cunjak 1986, Rand 1950, Emery et al. 1972), green frog (*R. clamitans*) (Pope 1944, Pinder et al. 1992, Lamoureux and Madison 1999), and bullfrog (*R. catesbeiana*) (Stinner et al. 1994).

Oxygen depletion can kill or physiologically stress frogs overwintering in ice-covered ponds (Bradford 1983). Recent field studies have shown that overwintering frogs remain active under ice (Friet 1993; Stinner et al. 1994), and that localized depletion of dissolved oxygen may trigger movement. However, movements also could represent avoidance of low temperatures. For frogs submerged under ice, movement between layers of naturally occurring temperature and oxygen gradients may be necessary for survival (Tattersall and Boutilier 1997). Terrestrial overwintering may minimize the risk of oxygen depletion but may increase risk of dessication, freezing, or predation.

Ranid frogs may aggregate in large numbers at overwintering sites (Breckenridge 1944), so disturbing unrecognized overwintering sites may compromise entire populations. Recent indications that amphibians have declined on a global scale (Wake 1991) have increased the need for a more comprehensive understanding of overwintering patterns. To date, there have been no thorough studies of overwintering sites of Columbia spotted frogs (*R. luteiventris*). Our objectives were to identify overwintering sites and to determine temperatures and dissolved oxygen levels associated with these sites of Columbia spotted frogs in northeastern Oregon.

Methods

We monitored overwintering activity in radio-tagged Columbia spotted frogs from September 1997 until March 2000. We radio-tagged 10 frogs (6 females, 4 males) in 1997, 42 frogs (27 females, 15 males) in 1998, and 48 frogs (28 females, 20 males) in 1999. Frogs were captured in three habitat types: (1) Grande Ronde River, (2) ponds located in the upper Grande Ronde River watershed, Union County, Oregon, and (3) Crawfish Lake, a 125,600 m^2 lake (10 m deep) in the North Fork John Day River watershed of Grant County at 2040 m in elevation. The ponds in the

[1]Author to whom correspondence should be addressed. E-mail:ebull@fs.fed.us

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Grande Ronde River watershed were 95-4132 m^2 in size and within 200 m of the river (within the floodplain), except Rainbow pond, which was a large (28,526 m^2) and isolated pond on a ridge 3600 m from the river. The ponds were 0.9-3 m deep, and 915-1800 m in elevation. Winter air temperatures in these study areas were usually below freezing from December through February, with extremes of -30°C in December 1998. All ponds were permanent and in forested habitats.

Frogs were captured with dip nets along the river and pond shores in August and September of each year. Frogs were sexed and weighed to the nearest 0.2 g, and those weighing ≥ 22 g were fitted with a radio transmitter. Transmitters (model BD-2G, Holohil Systems Inc., Ontario, Canada) weighed 1.8 g, lasted 6 months, and had a range of 200-300 m. Each transmitter was glued to a flat 6-mm wide satin ribbon harness that was fitted around the waist of each frog (Bull 2000). Frogs were checked monthly for abrasions and harness fit when accessible.

Frogs were monitored once each week, from capture until the transmitter failed, the frog slipped out of the harness or was killed, or the signal could not be detected. We attempted to confirm the frog's location visually; if the frog was under ice, we estimated the location to within 0.3 m of the frog. Each time a frog was located, we recorded the date, aquatic habitat type, distance from the previous location, snow depth, and the percent of water surface area covered with ice. Overwintering sites were classified as ice-covered ponds, partially-frozen ponds, temporary backwaters, seeps, and lotic habitats (creeks and rivers). Distance traveled to the overwintering site was the linear distance from the original point of capture to the overwintering site. Water depth and distance from shore were recorded at each overwintering site. Frogs that could not be located with ground tracking were searched for with a fixed-wing airplane within a 5-km radius of the last known location of the frog within 2-6 wk after the frog was missing.

Water temperature and dissolved oxygen were determined in 1998 and 1999; in 1997, we identified overwintering sites only. Water temperature and dissolved oxygen (DO) were measured with a portable YSI meter (Model 55) and were recorded as close to each frog as possible (typically within 0.3 m) once ice formed on a pond. Water temperature and DO were also recorded at one fixed location in each ice-covered and partially-frozen pond each week as long as frogs were monitored in that pond in 1998 and 1999. We selected sites for the fixed locations on the opposite end of the pond from the frogs' locations and at the same distance from the shore that the frogs were located. Readings were taken approximately 10 cm above the pond bottom for both frog and fixed locations. Readings at fixed locations were intended to represent a sample of water temperature and DO in each pond, but were not recorded at seeps, temporary backwaters, and under banks. Seeps and backwaters were too small to get readings away from the frog, and banks were inaccessible. Readings at fixed locations in lotic habitats were not collected after an interval of 2 wk because water flow resulted in few differences between fixed and frog locations. A 10-cm diameter ice auger was used to reach water for water temperature and DO readings when ice was present.

Values of DO and water temperature measured at fixed points and at frog locations in ice-covered and partially-frozen ponds were compared using Wilcoxon matched-pairs signed ranks tests (Snedecor and Cochran 1980). Due to the question of independence of multiple locations on the same frog, the mean water temperature and DO for each frog and for each fixed location in one pond during the time period they were monitored were used in the analysis. If more than one frog was monitored at a pond, only data for the frog that was monitored the longest were used; we only monitored the same data at one fixed location in each pond. We used Wilcoxon matched-pairs signed ranks tests to compare DO and water temperature recorded at one frog in Rainbow pond and Crawfish Lake in 1999 when frogs in both ponds were monitored (data paired by date). Distances that each frog traveled between successive visits were compared at Rainbow pond and Crawfish Lake before and after the surface froze and between sites using t-tests after transforming the data (base-10 log transformation) to achieve normality. The level of significance was set at $P = 0.05$.

Results

From 1997 to 1999, 68 frogs were radio-tagged in ponds and 32 frogs tagged along rivers. Eight, 23, and 35 frogs were tracked to overwintering sites in 1997, 1998, and 1999; the remainder of

the frogs died, slipped transmitters, or had transmitters fail. Of the 66 frogs monitored to overwintering sites, 29 overwintered in ice-covered ponds, 19 in partially-frozen ponds, 15 in lotic habitats, 2 in temporary backwaters, and 1 in a seep (Figure 1). Seven of 46 frogs originally captured in ponds and 9 of 20 frogs originally captured in the river, moved a mean distance of 275 ± 4.3 m to a different site to overwinter between 21 September and 13 October. The other 50 frogs overwintered in the original capture site.

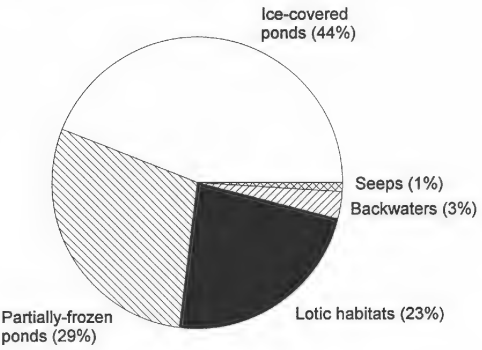

Figure 1. Proportional use of overwintering sites of Columbia spotted frogs, 1997-2000.

Ice-Covered Ponds

Twenty-nine frogs overwintered in seven ice-covered ponds (Figure 1). Mean area of these ponds equaled 22,275 ± 56.4 m^2, and mean depth equaled 2.4 ± 0.6 m. Surfaces froze for all ponds by late November or early December each year and thawed between March and May. Once the pond surface froze, DO declined over the winter (Table 1). For frogs that overwintered under the ice, DO levels were significantly higher (Z = -2.53, P = 0.012) at frog locations than at fixed points, but water temperatures did not differ statistically (Table 1).

Because of their large sizes, only Rainbow and Crawfish offered opportunities for extensive frog movements. Frogs under ice at Rainbow moved throughout the winter; 90% of locations of 14 frogs were within 1 m of shore and in water < 1m deep. Distances traveled by frogs before and after the pond's surface froze were significantly different in 1997 (t =-2.10, 97 df, P =0.039) and in 1999 (t = 2.25, 29 df, P < 0.001) but did not differ statistically in 1998 (Figure 2). After ice covered the surface of the pond, 71% of the locations of 14 frogs were found on the north shore, which lacked

TABLE 1. Mean (±SE) measurements of dissolved oxygen (mg/l) and water temperature (°C) at frog locations and at fixed points in ice-covered ponds, partially-frozen ponds, and lotic habitats used for overwintering by Columbia spotted frogs in northeastern Oregon, 1999-2000.

Variable/ month	Ice-covered ponds	Partially-frozen ponds	Lotic habitats
		Dissolved oxygen	
December			
Frogs	7.2 ± 0.6	4.6 ± 0.5	11.9 ± 0.4
Fixed	1.6 ± 0.6	4.0 ± 0.4	
January			
Frogs	7.0 ± 0.5	4.4 ± 0.4	11.4 ± 0.3
Fixed	2.1 ± 0.4	2.5 ± 0.4	
February			
Frogs	5.8 ± 0.7	4.7 ± 0.8	10.9 ± 0.6
Fixed	1.0 ± 0.2	2.1 ± 0.5	
		Water temperature	
December			
Frogs	0.6 ± 0.1	3.7 ± 0.3	0.4 ± 0.1
Fixed	0.4 ± 0.1	1.3 ± 0.2	
January			
Frogs	0.3 ± 0.1	2.4 ± 0.3	0.4 ± 0.0
Fixed	0.2 ± 0.0	0.6 ± 0.1	
February			
Frogs	0.5 ± 0.1	2.6 ± 0.3	0.8 ± 0.1
Fixed	0.5 ± 0.1	0.6 ± 0.3	
No. of frogs at each habitat	8	8	10

emergent or submergent vegetation. In contrast, before ice formed, 97% of the locations of these 14 frogs were found on the west, east, and south shores where emergent vegetation grew.

In contrast, frogs at Crawfish Lake moved significantly shorter distances than frogs at Rainbow pond (t = -5.64, 71 df, P < 0.001) after the surface froze in 1999 (Figure 2). DO did not differ significantly between the ponds, although water temperature was significantly higher at Rainbow pond (Z = -2.20, P = 0.028). Frogs in Crawfish Lake moved to a specific overwintering location by mid-October, where they remained hidden under logs in water < 30 cm and within 50 cm of the shore for the winter. Distances traveled by frogs after ice formed were significantly less than before ice formed ((t = -5.64, 97 df, P < 0.001; Figure 2).

Hollow chambers occurred under banks along the edge of two ice-covered ponds, and all 12 radio-tagged frogs in these ponds overwintered in

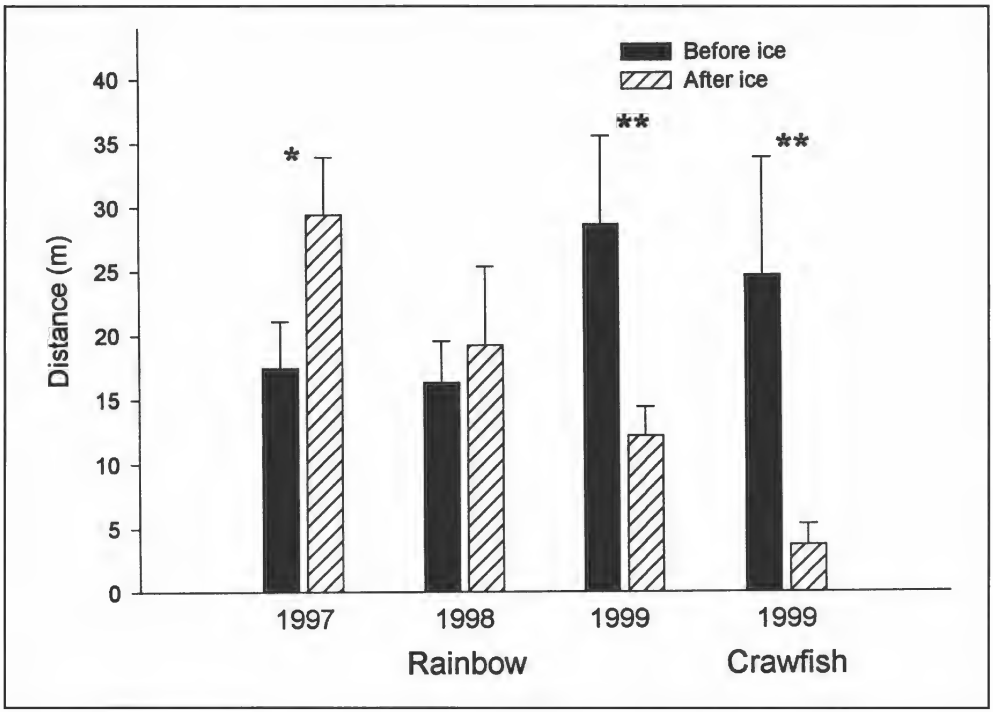

Figure 2. Mean distances (SE shown by lines) traveled by radio-tagged Columbia spotted frogs between consecutive locations before and after ice formed at Rainbow pond during three winters (1997-1998, 1998-1999, and 1999-2000) and at Crawfish Lake during one winter (1999-2000); *: $P < 0.05$, **: $P < 0.001$.

those chambers. Banks had access points through entrance tunnels 10-20 cm in diameter and at or below the water surface. Frogs first entered bank sites between 7-8 October 1997, 12-26 October 1998, and 15-23 November 1999. In 1997 and 1999, frogs remained in the banks for the entire winter. In 1998, when the water level was 25 cm higher, frogs moved between the bank sites and the pond during the winter. This higher water level resulted in the entrances to the five bank sites being submerged, thus accessible to the frogs under the ice. Five of the six frogs monitored in 1998 used more than one bank site in the winter. All frogs overwintered in situations with an air pocket over water in the situations where we could examine the chamber under the bank.

Partially-frozen Ponds

Nineteen frogs overwintered in seven ponds with partially-frozen surfaces that typically had small areas (0.5-10 m^2) of open water surrounded by ice all winter. These ponds had a mean surface area of 793 ± 28.0 m^2 and a mean depth of 1.2 ± 0.4 m. The majority (95-99%) of pond surfaces froze in November and thawed in March. Open water resulted from an upwelling of warmer water from springs in these otherwise frozen ponds. Frogs occurred in these areas of warmer water at > 90% of the locations after most of the surface of the ponds froze. Water was significantly warmer and DO significantly higher at frog locations than at fixed locations ($Z = -2.37$, $P = 0.018$; $Z = -2.37$, $P = 0.018$) (Table 1).

All 19 frogs were in the warmer water at the overwintering sites between 7 September and 9 November each year. Frogs stayed in the ice-free area all winter and usually traveled < 6 m from the previous location each week. Water depth at the overwinter sites ranged from 10-80 cm; distance from shore ranged from 20-600 cm.

Lotic Habitats

Twelve frogs overwintered in the Grande Ronde River and three in creeks flowing in and out of Crawfish Lake. The 12 frogs in the river overwintered under banks (n = 9), in a pool 1.2 m deep (n = 1), along the river edge (n = 1), and hidden in the submerged grass on the outside of a bank (n = 1). DO levels were high in the river throughout the winter compared to ponds (Table 1). The river surface was typically frozen between late December and mid-February, although water flowed under the ice all winter. Of the nine frogs overwintering under banks, six were under an overhanging ledge, two were between the original bank and a piece of sod that had collapsed into the river, one was in a 6-cm diameter hole that went back into the bank, and one was under a log in the bank. An air-water interface occurred at each site. Water depth at bank sites ranged from 8 to 90 cm. Frogs that overwintered under banks moved < 5 m between consecutive visits, while two of the three frogs not protected by banks moved 470 and 500 m downstream in December and January.

The flow of the two creeks where three frogs overwintered kept the water surface from freezing all winter. One site remained open to the air, and the second site was under 1.7 m of snow. All three frogs remained under logs in 25-40 cm of water and were 30-100 cm from shore while at these sites. DO levels remained high (8.5-10.0 mg/l) at both creeks all winter.

Temporary Backwaters and Seeps

Two frogs overwintered in backwaters (2 and 10 m^2 in size) off the main river where some flow existed during winter but none during late summer. One frog remained under a log in one backwater 18 cm deep, and the other frog was under a bank 57% of the time that it was located and in the open water (25 cm deep) during the remainder. Both frogs moved < 2 m between consecutive locations within the backwaters.

One frog moved 125 m from Rainbow pond to a seep on 11 October 1999 where it overwintered. The seep occurred under the root wad of a fall tree in a forested stand of Engelmann spruce (*Picea engelmannii*) with grass and moss ground cover and small pools of standing water. The water under the root wad never froze during the winter, although the DO dropped below 1.0 mg/l during February within 0.5 m of the frog.

Discussion

Columbia spotted frogs in northeastern Oregon overwinter in an environment with relatively harsh conditions, where freezing of the frogs is a risk. Strategies for overwintering survival include cold-induced reductions in activity levels and metabolic rates (Boutilier et al. 1997), and avoidance of freezing and anoxic conditions. Additional risks in some aquatic environments include predation and scouring. To avoid these risks, Columbia spotted frogs overwintered under banks and in ice-covered ponds, and maintained considerable mobility in water below 3°C.

In ice-covered ponds, scouring is not present and the risk of predation (except by fish) and freezing is low, but DO may be a determinant of survival. Anaerobic metabolism is adequate for anurans to survive brief anoxic periods; they must move to areas of high oxygen content for long-term survival (Penny 1987). High mortality was observed in mountain yellow-legged frogs (*R. muscosa*) overwintering in ice-covered lakes at high elevation due to oxygen depletion (Bradford 1983). Winterkill of frogs is frequent when snow-covered ponds result in an oxygen deficient environment (Pinder et al. 1992).

In partially-frozen ponds, warm water upwellings keep a portion of the surface ice-free. This would allow light to reach the pond's primary producers, thus increasing DO levels. Frogs may prefer higher temperatures because they enhance locomotory function and maintain conditions that allow air-breathing.

Under conditions in which sufficient DO is available (i.e., normoxic), submerged frogs prefer to remain as warm as possible (Tattersall and Boutilier 1997, 1999). This behavior might explain the significantly higher water temperatures at frog locations compared to fixed locations that we observed. The ability to remain active throughout the winter allows the frogs to take advantage of favorable areas in thermally and chemically stratified bodies of water (Tattersall and Boutilier 1997, 1999).

Although some aquatic plants can continue photosynthesis under ice and snow, the seasonal dieback of aquatic plants often results in elevated detrital decomposition and a net reduction in

oxygen (Marchand 1996). Rose and Crumpton (1996) found that sites within emergent stands of macrophytes in ponds had extremely low DO concentrations and were almost continuously anoxic; the highest DO levels were in open water. In our study, movements of frogs and their preferences for the north shore after ice formed at Rainbow may represent a response to higher levels of DO because aquatic vegetation was absent on the north shore.

Alternatively, lack of movement by frogs at Crawfish Lake after ice formed (with DO levels equivalent to those at Rainbow pond) may have been a response to predation risk by eastern brook trout (*Salvelinus fontinalis*). Emery et al. (1972) found frogs in splake *(Salvelinus fontinalis X S. namaycush*) and rainbow trout (*Oncorhynchus mykiss*) stomachs in ponds in the winter. In contrast, frogs at Rainbow, which lacked both fish as predators and logs as cover, were not located in specific overwintering sites.

Frog preference for shallow water near the shore in ice-covered ponds could be a response to higher levels of DO that occur at the ice-water interface (Boutilier et al. 1997) or a means of avoiding predatory fish at Crawfish Lake. In addition, lakes may be markedly hypoxic at depths of 2-4 m (Boutilier et al. 1997).

Unfrozen water and an air pocket were present in the bank sites that we could access. Bank sites may allow frogs to overwinter in ponds where DO levels in open water fall below 2.0 mg/l for extended periods.

In lotic habitats, where DO levels and freezing are less likely, unpredictability of flow and predators may present more substantial risks to overwintering frogs. Frogs under banks along rivers avoid both scouring and predation.

Different overwintering strategies in Columbia spotted frogs appear to result from tradeoffs among factors that may compromise survival at different sites. Our data, which focused on the potential risks posed by oxygen limitation and freezing, indicate that selected sites generally minimized the risks of both. Oxygen limitation may be a prominent risk factor at high elevation sites because these typically are capped by ice. Additional information is still needed on the submerged DO levels that this species can tolerate during the winter, the exact nature of bank sites, and the extent that predation plays in the selection of overwintering sites.

Acknowledgements

Jay Shepherd conducted the statistical analyses. Lisa Hallock and Peter Hovingh reviewed an earlier draft of the manuscript. Frogs were handled under a scientific taking permit from the Oregon Department of Fish and Wildlife.

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Received 17 April 2001
Accepted for publication 9 November 2001

Andrew B. Carey,[1] Pacific Northwest Research Station, USDA Forest Service, 3625 93rd Avenue SW, Olympia, Washington 98512

Wes Colgan, III, School of Biological Sciences, Louisiana Tech University, Ruston, Louisiana 71272

James M. Trappe, Department of Forest Science, Oregon State University, Corvallis, Oregon 97333

and

Randy Molina, Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon 97330

Effects of Forest Management on Truffle Abundance and Squirrel Diets

Abstract

Thinning and retention of biological legacies (large live, dead, and fallen trees and their associated biota) during clearcutting are two practices to promote development of late-seral attributes in second-growth forests. We evaluated the effects of these practices on production of truffles and use of truffles as food by northern flying squirrels and Townsend's chipmunks in 55-65-yr-old Douglas-fir forests in the Puget Trough of Washington. Truffles were collected at 6-wk intervals from March 1993 through December 1995. Feces were collected from flying squirrels and chipmunks in fall and spring, 1991-1995, and relative frequencies of truffle genera and vascular plant parts therein were determined. Mean standing crop biomass of truffles did not differ between thinned and legacy forests. However, dominant genera of truffles in the soil and in feces did. Truffles in soil and in flying squirrel diets were more diverse in legacy than in thinned forest. *Gautieria*, a consistently important component of flying squirrel diets, but not chipmunk diets, was more abundant in legacy than in thinned forest. *Melanogaster*, eaten by both chipmunks and flying squirrels, was more abundant in thinned than in legacy forest, as were vascular plants. Chipmunks consumed large amounts of vascular plant material. Flying squirrels also consumed plant parts in thinned forest, but they did not consume measurable amounts of plant materials in legacy forest. Flying squirrels consumed a greater diversity of truffles than we found with intensive random sampling. The ability of flying squirrels to find truffles, their propensity to ingest all species of truffles, their excretion of viable spores, and their wide travels makes them important in maintaining the diversity of ectomycorrhizal fungi.

Introduction

Mycorrhizal fungi enhance the ability of trees to absorb water and nutrients from soil and they move photosynthetic carbohydrates from trees to the mycorrhizosphere. In turn, this carbon supports a vast array of microbes, insects, nematodes, bacteria, and other organisms in the soil (Fogel 1988, Ingham and Molina 1991). Sporocarps of hypogeous ectomycorrhizal fungi (hereafter referred to as truffles) are food for diverse animals worldwide (Fogel and Trappe 1978, Maser et al. 1978, Viro and Sulkava 1985, Malajczuk et al. 1987, Blaschke and Baumler 1989, Launchbaugh and Urness 1992, Claridge and May 1994, Carey 1995). Truffles attract animals by producing aromatic compounds (Fogel and Trappe 1978). Most truffles consumed by animals in temperate forests are formed by ectomycorrhizal fungi in symbiotic association with the roots of Pinaceae, Fagaceae, Betulaceae, Myrtaceae, and Salicaceae (Molina et al. 1992). Animals consume all or part of a truffle (Fogel and Trappe 1978) including spores, bacteria, and yeasts that live in the truffle (Li et. al. 1986). These spores, yeasts, and bacteria pass through the digestive tract unharmed and are deposited in feces in new locations (Trappe and Maser 1976). Precipitation then moves fecal contents into the soil where the fungi colonize new roots (Trappe and Maser 1976). The mammals that disseminate spores also serve as prey for owls, raptors, and mustelids (Carey et al. 1999a, Carey 2000a). Thus, this food web of trees, truffles, and mammals may be considered a keystone complex (Daily et al. 1993) particularly indicative of forest ecosystem function in the Pacific Northwest (Carey et al. 1999a).

The major mycophagists in the Pacific Northwest are the northern flying squirrel (*Glaucomys sabrinus*), Douglas' squirrel (*Tamiasciurus douglasii*), and Townsend's chipmunk (*Tamias townsendii*). The Douglas' squirrel and Townsend's chipmunk are known to store and eat various foods besides truffles, including conifer seed. As adaptations to seasonal food shortages, the Douglas'

[1] Author to whom correspondence should be addressed. E-mail: acarey@fs.fed.us

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squirrel maintains small territories and stores conifer cones. The chipmunk maintains small home ranges in shrubby areas that provide food (berries, nuts, and seeds) and cover from predation and sometimes hibernates in winter (Carey 2001). The flying squirrel seems to depend more on truffles than the other squirrels and its densities seem correlated jointly with truffle biomass and diversity (Carey 1995). Flying squirrel densities in old forests vary regionally, in a manner opposite to what would be expected based on total truffle abundance alone. Densities in natural forests in the North Cascades (0.2/ha) and Olympic Peninsula (0.5/ha) of Washington, where truffle biomass is unusually high (North et al. 1997), were low compared to the Western Cascades (2.3/ha) and Coast Ranges (1.9/ha) of Oregon (Carey 1995) where truffle abundance is moderate (Luoma 1991), and similar to those in managed forests in the Puget Trough of Washington (0.5-0.8/ha) (Carey 2001), where truffle abundance is low (Colgan et al. 1999). The lack of correspondence between abundance of flying squirrels and truffles may be due to differences in seasonal production of truffles, nutritional value of different species of truffles, and lack of correlation between abundance and diversity of truffles. For example, in areas of Washington where truffle biomass was high, diversity was low with 95% of biomass in one species, *Elaphomyces granulatus* (North et al. 1997).

The ecology of truffle production is poorly understood. Peak truffle production in the Pacific Northwest occurs during spring and fall but varies markedly from year to year (Fogel 1976, Hunt and Trappe 1987, Luoma et al. 1991) and with forest type and age (Vogt et al. 1981; Luoma 1989, 1991; Luoma et al. 1991; O'Dell et al., 1992; Amaranthus et al. 1994; Pilz and Molina 1996). In the Olympic and North Cascade mountains of Washington, truffle biomass was five times greater in old growth (4.0-4.5 kg/ha) than in second-growth managed forest (North et al. 1997). In the Western Cascades of Oregon, however, truffle biomass was <1 kg/ha in old growth, but >2 kg/ha in second growth (Jane E. Smith, USDA Forest Service, personal communication). In naturally young Douglas-fir (*Pseudotsuga menziesii)* forest in a nearby study, biomass (1.2 kg/ha) was similar to that in old growth (1.6 kg/ha) (Luoma 1991). Truffles were abundant in second-growth Douglas-fir in the Oregon Coast Range, 2.3-5.4 kg/ha (Fogel 1976) and 2.0-3.2 kg/ha (Hunt and Trappe 1987). Thus, truffle production varies greatly in space and time. Some truffles are available year-round, but there have been no definitive studies of truffle abundance in summer and winter (Fogel 1976, Hunt and Trappe 1987, North et al. 1997).

Most studies of mycophagy have lasted <1 yr and do not explain how the functional relationship between squirrels and truffles is maintained in winter and summer, seasons when truffles may be scarce. Nor do these few studies explain how the flying squirrel can compete for truffles with Douglas' squirrels and Townsend's chipmunks in winter, when food (except stored food) generally is scarce and truffles still are the principal food of flying squirrels. For flying squirrels, truffle production during winter may be critical (Carey 1995). Flying squirrels are not only at high risk from predators while foraging for truffles on the ground (Wilson and Carey 1996) but also at risk to rapid loss of metabolic heat because of their habits of nocturnal activity, arboreal travel and gliding, and their high surface area relative to body mass. Flying squirrels must employ an optimal foraging strategy that allows them to minimize time on the ground and time of exposure to low temperatures. They also change dens regularly as an additional predator-avoidance strategy (Carey et al. 1997). The benefits of being able to locate and extract truffles quickly to avoid predation and minimize energy expenditure is somewhat offset by the low nutritive value of truffles and travel time to foraging sites (Cork and Kenagy 1989, Claridge et al. 1999, Carey 2000a).

The nutritional value of truffles for squirrels is low (Cork and Kenagy 1989, Claridge et al. 1999). Nevertheless, the three common squirrels in the Pacific Northwest feed on truffles throughout the year, primarily the genera *Rhizopogon, Melanogaster,* and *Hysterangium* (Maser et al. 1978, 1985, 1986; Carey, 1995; Carey et al. 1999a). These truffle genera are heavily consumed by mycophagists in general (North et al. 1997). Truffle diversity may be important in providing an adequate diet for mycophagists because truffles may differ in nutrient content (Claridge et al. 1999). Truffle species richness does not vary regionally, but apportionment of biomass among species does. Forty-three species occurred across western Washington (North et al. 1997), but a single species (*Elaphomyces granulatus*) accounted for 95% of biomass. Forty-seven species occurred across the

Western Cascades of Oregon, with five species accounting for 73% of the biomass (Luoma 1991). Diets of squirrels may reflect differential consumption of truffles. Even where biomass of *Elaphomyces* was high (North et al. (1997), *Rhizopogon* dominated in squirrel diets (Carey 1995). The food value of *Elaphomyces* is near the minimum on which squirrels are able to maintain themselves as a sole source (Cork and Kenagy 1989) and flying squirrels lose weight on a diet of *Rhizopogon vinicolor* (Claridge et al. 1999). Thus, a diet of multiple fungi may be important to mammalian mycophagists (Claridge et al. 1999).

Management may affect truffle production, but the effects are not clear. Management seems to affect production of truffles by different species differently. Production of truffles by *Gautieria* (and *Hysterangium*) is reduced by thinning in the short-term (Colgan et al. 1999). Fruiting of *Melanogaster*, like *Hysterangium setchellii*, is favored by thinning (Colgan et al. 1999). Several factors may underlie low truffle production by certain species in thinned forest. Species that form hyphal mats may be more susceptible to mechanical damage by logging operations. Thinning may change microenvironment to the detriment of these species. *Hysterangium* and *Gautieria* were significantly less frequent in shelterwood stands in California 17 and 20 yr after timber harvest (Waters et al. 1994). Similarly, *Hysterangium* spores were infrequent in feces of Siskiyou chipmunks (*T. siskiyou*) in shelterwood stands in southwestern Oregon (McIntire 1984). *Gautieria* mats were common only in the rooting zone of retained old-growth trees 2 yr after a shelterwood harvest in the Oregon Western Cascades (Aguileria et al. 1993). Shelterwood harvests remove a greater proportion of trees than does thinning and considerable time may be required after disturbance for some fungal taxa to recover and fruit. Reduced biomass of *E. granulatus* in managed compared to natural old forests may be a consequence of reduced organic layers and root density in managed forests (North and Greenberg 1998). Other species, such as *Rhizopogon parksii*, are not associated with organic layers at the cool, moist end of the Western Hemlock Zone (North et al. 1997, North and Greenberg 1998). At the opposite extreme (hot, dry) in southwestern Oregon, there is a close association between truffles of various species and decaying logs on the forest floor (Amaranthus et al. 1994). Concerns about the effects of forest management on fungi led to special protection for fungal species thought to be associated with late-successional forests (FEMAT 1993, USDA and USDI 1994, Castellano et al. 1999). Most of these species, however, were newly described with little information on their ecologies. Concern about the effects of forest management on the spotted owl (*Strix occidentalis*) and its primary prey, the northern flying squirrel—also a consumer of truffles and disperser of truffle spores—was the primary motivation behind massive changes to federal land management in the Pacific Northwest (FEMAT 1993).

Our objective was to determine the effects of forest management on production of truffles and on diets of northern flying squirrels and Townsend's chipmunks in second-growth Douglas-fir forests in the Puget Trough of Washington. Specifically, we compared two alternative strategies for managing second-growth forests on long rotations (>70 yr) for late-seral attributes: 1) management with multiple thinnings to grow large trees and well-developed understories quickly, and 2) management with retention of biological legacies (old live, dead, and fallen trees and their associated biota) at harvest with no further management intervention.

Methods

Study Area

We studied four even-aged blocks of Douglas-fir forest totaling ≈150 ha chosen from 6,000 ha of second-growth forest on that part of Fort Lewis Military Reservation in Thurston County, in the southern Puget Trough of Washington. These forests were located in the Western Hemlock (*Tsuga heterophylla*) Zone wherein Douglas-fir often is dominant in young managed stands, but where Douglas-fir, western hemlock, and western redcedar (*Thuja plicata*) often are codominant in old natural forest (Franklin and Dyrness 1973). Soils were gravely sandy loams in glacial outwash plains. Topography was flat to gently rolling, 100-143 m above sea level. Average annual precipitation was 91 cm. Two blocks had been clearcut ca. 1927 and lightly thinned twice (1972 and late 1980s) to final retained densities of about 200 trees/ha (≈7 m between trees), hereafter referred to as thinned forest (Carey et al. 1999b). Thinned forest had 2-3% cover of coarse woody debris, few (<1/ha) residual old-growth trees, and dense

understories of salal (*Gaultheria shallon*), western brackenfern (*Pteridium aquilinum*), and western swordfern (*Polystichum munitum*). Two blocks were clearcut ≈1937 with retention of about six old-growth trees/ha and 10% cover of coarse woody debris, but received no further silvicultural treatment. Hereafter we refer to these blocks as legacy forest. Understories in legacy forest were variable and dominated by ground mosses. Salal and swordfern were patchily abundant in conjunction with canopy openings caused by laminated root rot (*Phellinus weirii*). We randomly selected 8 of the 16 available 13-ha stands, 2 per block, 4 from the legacy forest and 4 from the thinned forest. Within blocks, stands were >80 m apart; the forests were 4 km apart. Each stand had a central, square, surveyed sampling grid marked with plastic pipe and colored flagging (Carey et al. 1999b). Each grid consisted of 64 points (40 m apart) that were trapping stations for squirrels (Carey 2001) and references for locating fungal transects.

Fungal Sampling and Analysis

We sampled the forest floor for fungal sporocarps (truffles and mushrooms) 12 times (about every 6 wk) between April 1993 and December 1995. The December 1994 session, however, was interrupted by snow, thus 920 plots were sampled. We randomly chose a grid point, starting distance from the point, and direction for each sampling transect for each stand for each sampling occasion. Each transect consisted of 10 circular 4 m^2 microplots 10-m apart in each of the stands to be sampled (Luoma et al. 1991). First, mushrooms (primarily Boletaceae and *Russula* spp.) used as food by small mammals and obvious truffles were collected from the surface of each plot. Each plot was raked with hand tools to a depth of ≥5 cm into mineral soil to expose truffles. Each collection (one to several sporocarps of the same species in close proximity to one another on a single plot) was placed in a wax paper bag with a tag recording plot number, stand number, and other pertinent information. Field characteristics used in identification of sporocarps were noted. Plots were marked with plastic pin flags and the litter and duff were replaced. No plots were sampled twice. All fungal samples were dried the day of collection with a forced air dehydrator set at 49°C (Colgan 1997), transported to the Forestry Sciences Laboratory in Corvallis, Oregon, for identification, and weighed to the nearest 0.01 g. Voucher specimens were placed in the Mycological Herbarium at Oregon State University.

We calculated the frequency of encounter for each species found on the microplots. We measured taxonomic diversity as number of truffle species and as number of truffle genera. Biomass values were calculated for each transect as kg/ha dry weight transformed with log e (ln) to improve normality. Biomass was compared by using analysis of variance (ANOVA) and Fisher's protected least significant difference (PLSD) with the significance level of $P \leq 0.05$. We limited comparisons among diets and transects to genera composing >3% relative frequency in feces or >3% of biomass collected from plots.

Feces Collection and Analysis

Flying squirrels and chipmunks were live-trapped with standard methods (Carey et al. 1991), including two four-night sessions with 128 Tomahawk 201 traps/stand (two/grid point) in spring and fall, from fall 1991 to fall 1995. Fecal pellets were collected only at the first capture of an individual within a session to avoid feces containing ingested bait (peanut butter, molasses, and oats). One to five fecal pellets were collected from the anus and placed into a small glass vial which was sealed immediately to minimize contamination of by fungal spores in or around the trap site. We examined feces with the pooling method (Colgan et al. 1997). Briefly, samples from three to six animals of each species were randomly selected from the group of animals captured during one trapping period on one trapping grid. Pooled samples were macerated in small vials with approximately 1 ml of tap water (approximately four times the volume of the pellets) and shaken thoroughly. Then one drop of suspension was transferred to each of five microscope slides. One drop of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) was added, and the solution was covered with a 22 x 22-mm cover slip. We examined 25 randomly selected fields of view/slide at 400x magnification and recorded the items present in each field. Truffle spores were identified to genus according to Castellano et al. (1989). Mushroom spores were identified to family. Vascular plant fragments and insect parts were recorded. Miscellaneous and unidentifiable items occurring in <5% of the fields were grouped as unknown. Mean relative frequencies (RF) and standard errors (SE) of dietary items

were calculated by species of squirrel over trapping periods for each treatment. Abundances in plots were converted to ranks and compared to ranks in diets of chipmunks and flying squirrels with Spearman rank order correlations.

Results

We collected 590 truffles from 920 plots (3,680 m^2). We found 28 species: 19 in thinned forest, 7 of which were only in thinned forest, and 21 in legacy forest, 9 of which were only in legacy forest (Table 1). *Rhizopogon vinicolor* was the most frequent species and *Rhizopogon* was the most frequent genus in both forest types (Table 1). Three other species of *Rhizopogon* were found only in thinned forest. *Gautieria monticola* was seven times more frequent in legacy than in thinned forest. *Melanogaster tuberiformis* was six times more frequent in thinned forest. There were more species of *Leucogaster*, a genus important to both flying squirrels and chipmunks, in legacy than in thinned forest. Truffle collections were dominated (>3% relative frequency) by seven genera in legacy forest and five genera in thinned forest (Tables 1 and 2).

TABLE 1. Percent frequencies of sporocarps of hypogeous fungal species occurring with ≥3% relative frequency in plots in legacy forest and thinned forest in the Puget Trough, Washington, April 1993 through December 1995

Species[a]	Legacy	Thinned
Rhizopogon vinicolor	8.9	5.9
Tuber monticola	3.0	2.2
Hysterangium coriaceum	2.4	1.5
Hysterangium crassirhachis	2.1	1.1
Gautieria monticola	1.5	0.2
Endogone lactiflua	1.4	0.6
Hysterangium setchellii	1.1	2.4
Melanogaster tuberiformis	0.2	1.3
Leucophleps magnata	0.2	0.6
Rhizopogon hawkerae	–	3.3
Rhizopogon villosulus	–	0.9

[a]Taxa occurring with <3% relative frequency included: *Elaphomyces granulatus*, *Endogone pisiformis*, *Genabea cerebriformis*, *Genea intermedia*, *Glomus macrocarpum*, *Hymenogaster* sp., *Hymenogaster sublilacinus*, *Leucogaster candidus*, *L. citrinus*, *L. gelatinosus*, *L. rubescens*, *Leucophleps spinispora*, *Rhizopogon vulgaris*, *Truncocolumella citrina*, *Tuber anniae*, and two species new to science.

All species frequencies, however, were low, ranging from 0 to 8.9% of plots in any forest type (Table 1) and, thus, variances associated with mean standing crop biomasses were high. Standing crop biomass did not differ significantly between forest types for the 3 yr we sampled and averaged 0.48 kg/ha. Mean standing crop biomass ranged from 0 to 1.8 kg/ha over sampling periods with greatest values in spring and lowest values in winter, but 95% confidence intervals about the means overlapped for all sampling periods (Figure 1). The biomass of truffle collections totaled 176.1 g with 93.8 g from thinned forest and 82.9 g from legacy forest.

We collected 467 fecal samples from chipmunks and 185 from flying squirrels. The pellets of both species contained spores from families of hypogeous Ascomycetes, Basidiomycetes, and Zygomycetes and epigeous Ascomycetes and Basidiomycetes. *Rhizopogon* was the dominant fungus in the diets of both species in both forest types

TABLE 2. Relative frequencies of fungal sporocarp genera in soil, and spores and vascular plant parts in feces of *Glaucomys sabrinus* and *Tamias townsendii*, in thinned and legacy forest, 1991-1995.

	Glaucomys sabrinus				*Tamias townsendii*	
	Legacy		Thinned		Legacy	Thinned
Dietary components	Soil[a]	Diet[a]	Soil[a]	Diet[a]	Diet[a]	Diet[a]
Rhizopogon	40	22	47	31	27	20
Hysterangium	24	12	17	8	7	12
Melanogaster	1	10	6	20	–	9
Gautieria	6	13	1	6	–	–
Leucogaster	4	6	1	–	8	7
Leucophleps	3	5	3	–	15	10
Elaphomyces	1	6	–	–	–	–
No. truffle genera	7	7	4	5	5	4
Plant material	–	–	–	8	21	18

[a]A dash (–) indicates the taxa was not detected, or in the case of vascular plants in the soil columns, not recorded.

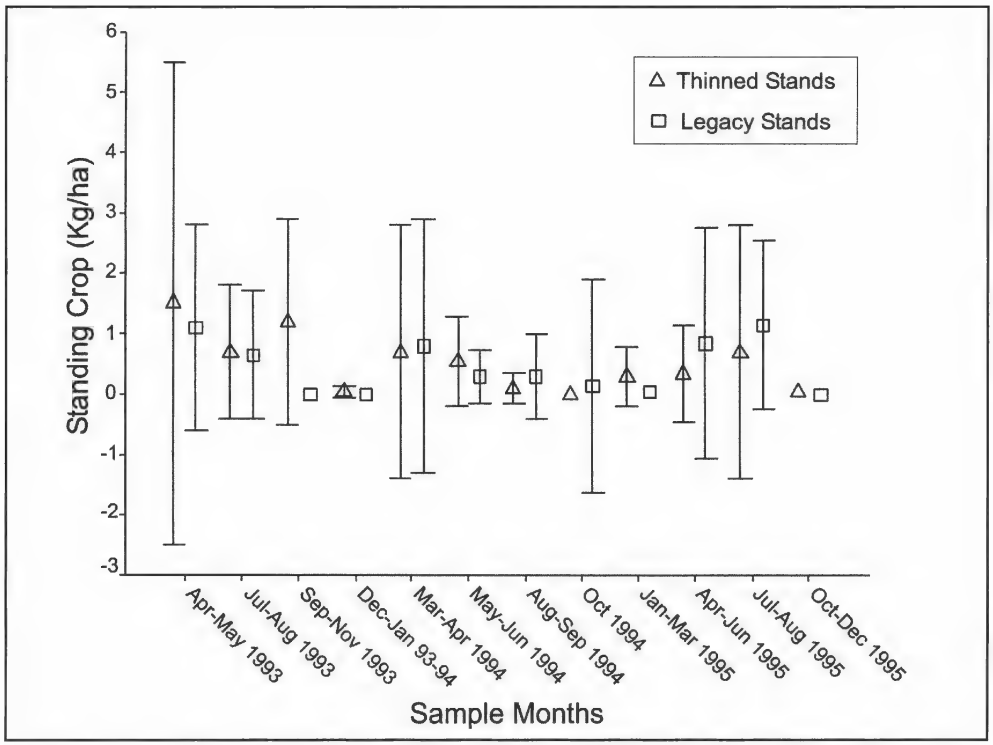

Figure 1. Means and 95% confidence intervals for estimated truffle biomass in second-growth Douglas-fir (*Pseudotsuga menziesii*) stands thinned twice with conventional thinning and never-thinned stands with biological legacies of old live trees, standing dead trees, and fallen trees from previous stands. December 1993-January 1994 sampling was interrupted by snowfall and could not be completed.

TABLE 3. Means and (standard errors) of relative frequencies of dietary fungal genera ≥3% relative frequency and vascular plant parts for *Glaucomys sabrinus* and *Tamias townsendii* thinned and legacy forests, 1991-1995.

	Glaucomys sabrinus		*Tamias townsendii*	
	Legacy	Thinned	Legacy	Thinned
Rhizopogon[a]	22 (1)	31 (5)	27 (4)	20 (5)
Hysterangium	12 (2)	8 (3)	7 (2)	12 (2)
Melanogaster	10 (2)	20 (4)	–	9 (1)
Gautieria	13 (4)	6 (2)	–	–
Leucogaster	6 (2)	–	8 (1)	7 (1)
Leucophleps	5 (3)	–	15 (4)	10 (2)
Elaphomyces	6 (3)	–	–	–
Plant material	–	8 (3)	21 (4)	18 (7)

[a] May include related taxa not distinguishable by spores alone

(Tables 2 and 3). Flying squirrels consumed *Gautieria*, even in thinned forest where we found no *Gautieria* sporocarps, and *Elaphomyces*, genera not present in the feces of chipmunks. *Leucophleps* had greater importance in chipmunk diets than in flying squirrel diets. Chipmunks consumed substantial amounts of vascular plant parts in both forest types, but flying squirrels consumed them primarily in thinned forest.Flying squirrel diets were more diverse in legacy than in thinned forest (seven vs. five frequent genera). Diet items were strongly correlated ($P < 0.001$) with abundance in plots for both flying squirrels ($r_s = 0.84$) and chipmunks ($r_s = 0.77$). Seasonal diets were correlated with seasonal abundances. We found in fecal pellets two genera of truffles, *Pachyphleous* and *Radiigera,* that we did not encounter in the field.

Discussion

Impacts of Management on Truffle Biomass in the Western Hemlock Zone

Management history had no discernable effect on truffle production in second-growth forest in the Puget Trough (Tables 1, 2). Compared to natural forests in Olympic Peninsula and North Cascades in Washington (North et al. 1997) and the Western Cascades in Oregon (Luoma 1991), Puget Trough second growth produced low biomasses of truffles (1-4.5 kg/ha vs. 0.5 kg/ha). Biomasses in the Puget Trough were similar to managed forests elsewhere in Washington, averaging 0.5 kg/ha over seasons, but ranging up to 1.8 kg/ha (Figure 1) versus 0.8 kg/ha (North et al. 1997). Second-growth forests in Oregon produced higher biomasses, averaging 2-5 kg/ha (Fogel 1976, Hunt and Trappe1987, Jane E. Smith, USDA Forest Service, personal communication). However, effects of forest management on truffle production in Oregon have been inconsistent (Fogel 1976, Hunt and Trappe 1987, Luoma 1991, North et al. 1997, Jane E. Smith, USDA Forest Service, personal communication). The overall effects of forest management on truffle biomass remain unclear.

Impacts of Management on Truffle Diversity

Species diversity was slightly greater in legacy than in thinned forest. A total of 28 species was present on plots totalling 3,680 m^2 in this study on Fort Lewis, but 48 species were present on 14,720 m^2 that included eight nearby experimental stands of similar age (Colgan et al. 1999). Thus, species richness seems to reach an asymptote of about 48 species with widespread sampling in the Pacific Northwest (Luoma 1991, North et al. 1997, Colgan et al. 1999). Six species accounted for 80% of the biomass in the Puget Trough, 5 for 73% in Oregon (Luoma 1991), and 1 species for 93% in the Olympic Peninsula and North Cascades in Washington (North et al. 1997). Truffle diversity in managed Puget Trough forests was similar to diversity in natural forests across the Western Hemlock Zone.

Management affected truffle diversity on Fort Lewis. More genera occurred in soil and in feces in legacy than in thinned forest. Four genera common in flying squirrel diets across the Pacific Northwest, *Gautieria, Leucogaster, Leucophleps,* and *Elaphomyces* (Carey 1995, Carey et al. 1999a), were less prevalent in soil and feces in thinned than in legacy forest. Production of truffles by *Gautieria* (and *Hysterangium*) was reduced by thinning in the short-term (Colgan et al. 1999). Apparently with conventional thinning, that effect is long lasting (Tables 1, 2) but not universal for species of *Hysterangium*. For example, *H. coriaceum* and *H. crassirhachis* were more abundant in legacy and *H. setchellii* was more abundant in thinned forest. *Leucogaster citrinus* and *Elaphomyces granulatus* are thought to be associated with late-successional forest (USDA and USDI 1994, Castellano et al.1999). These two species occurred in legacy forest but not in thinned forest. Fruiting of *Melanogaster*, like *H. setchellii*, was favored by thinning (Colgan et al. 1999). *Melanogaster* truffles were six times more frequent in soil and twice as abundant in flying squirrel feces in thinned than in legacy forest. Three of four *Rhizopogon* species occurred only in thinned forest. Several species of *Rhizopogon* are common in early stages of forest development and are often abundant on tree roots following disturbance (Molina et al. 1999). Seventy-one epigeous (mushroom-producing) fungi thought to be associated with late-successional forests were found on the Puget Trough sites (Carey et al. 1999b). Thus, it appears that many fungi thought to be associated with late-successional forest can persist in managed stands, particularly stands with legacies from old-growth forest. Management does not decrease the diversity of fungi; rather, it may promote a diversity of fungi.

Truffles and Squirrels

Our study was the first multiyear study of mycophagy in the USA. Diets were similar to those reported previously (Maser et al. 1978, 1985, 1986; Carey 1995; Carey et al. 1999a). Our sampling intensity for plots was high compared to most studies, yet flying squirrels found as many genera during one 2-wk period as we found in 3 yr. Flying squirrels moved farther than chipmunks to forage (Carey 1995, 2000a). This mobility and a widely dispersed, but clumped, distribution of *Gautieria* truffles may explain the lack of consumption by chipmunks and the rarity of *Gautieria* in our soil samples compared to the prevalence of *Gautieria* in the flying squirrel diet. Squirrels used many species in proportion to their occurrence. Animals that forage by smell will detect the

odor nearest to them first and the truffles species with the most uniform and frequent distribution should dominate the diet, as *Rhizopogon* does. *Rhizopogon* may not produce as large a localized biomass of truffles as *Elaphomyces* (North et al. 1997), or even the most nutritious truffles (Claridge et al. 1999), but *Rhizopogon* produces truffles with high frequency at local scales in natural and managed forests over a wide geographic area (Table 2; Carey 1995, Molina et al. 1999). High mobility of flying squirrels compared to chipmunks and Douglas' squirrels (Carey 2001) and their willingness to consume all species of truffles explains their ability to compete with chipmunks and Douglas' squirrels for a limited truffle resource.

Total taxonomic diversity of truffles differs little among five of the six physiographic provinces in western Oregon and Washington (the Southern Cascades of Washington have not been studied). The Olympic Peninsula and North Cascades forests, however, seem to have been dominated more by a single species than elsewhere. Flying squirrel diets were rich in Puget Trough legacy forests (seven commonly occurring truffle genera) compared to similarly managed forests on the Olympic Peninsula (four genera) and similar in diversity to diets in old-growth forests on the peninsula (six genera). Diets in thinned forests in the Puget Trough had the same number of genera (four) as diets in the legacy forests on the Olympic Peninsula. Flying squirrel diets in the Puget Trough and on the Olympic Peninsula had fewer genera than flying squirrel diets from the warmer, drier, southern Oregon Coast Range (12 genera in old growth and 9 genera in extensively managed forests) (Carey 1995, Carey et al. 1999a).

Flying squirrel abundance varied with truffle abundance in northeastern California (Waters and Zabel 1995). In southwestern Oregon, flying squirrels foraged where coarse woody debris was abundant (Carey et al. 1999a) and coarse woody debris was positively correlated with truffle abundance (Amaranthus et al. 1994). However, on the Olympic Peninsula, flying squirrel abundance was correlated more with understory development (Carey 1995) and abundance of mast-bearing trees (*Acer circinatum* and *A. macrophyllum*)—ancillary sources of high quality food—than with coarse woody debris (Carey and Harrington 2001). In contrast, flying squirrels were 1.6 times more abundant in the legacy than in thinned forest, whereas chipmunks were 4.4 times more abundant in thinned forest (Carey 2000b, 2001). The value of shrubs as food and cover explains differences in chipmunk abundance (Carey 2000b, 2001), but not differences in flying squirrel abundance, given that (1) truffle biomass was equal in the two forest types, (2) flying squirrels consumed all species of truffles (Colgan 1997), (3) truffles are nutritionally poor (Cork and Kenagy 1989, Claridge et al. 1999), and (4) vascular plant parts consumed by flying squirrels (Thysell et al. 1997) have high nutritive value (Cork and Kenagy 1989). Locally, flying squirrel abundance may be determined by (1) availability of dens (Carey et al. 1997; Carey 2001), (2) habitat-mediated predation (Carey et al. 1992; Wilson and Carey 1996), (3) competition with chipmunks and Douglas' squirrels in environments simplified by forest management (Carey and Harrington 2001), and (4) ancillary food sources (Ransome and Sullivan 1997, Thysell et al. 1997, Carey and Harrington, 2001). Our results support the hypothesis that simultaneously high populations of northern flying squirrels, Townsend's chipmunks, and Douglas' squirrels in the Douglas-fir keystone complex—a characteristic of old, natural forests (Carey 1995)—results from ecological processes of development of habitat breadth and niche diversification (Carey et al. 1999a) and not from a single limiting factor (Carey 2001, Carey and Harrington 2001).

Acknowledgments

Funding was provided by the U.S. Army, Fort Lewis Military Reservation, the USDA National Research Initiative Competitive Grants Program (Grant No. 9401095), and the USDA Forest Service, Pacific Northwest Research Station. We thank >80 volunteers who contributed >2,000 hours to sampling truffle plots, often under adverse conditions. Special thanks to D. Thysell for field and logistical assistance and to M. Myrdall, P. Molina, and J. Eblin for data entry. Many thanks to A. Claridge, D. McKay, J. Smith, M. Kiel, C. Cray, D. Luoma, and D. Pilz who each contributed in numerous ways. We thank A. Claridge, R. Forbes, D. Luoma, F. Rhoades, and M. Vavrek for careful reviews of an early manuscript.

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Received 7 September 2001
Accepted for publication 14 December 2001

Brian W. Moser,[1] Potlatch Corporation, Hybrid Poplar Program, Boardman, Oregon 97818-0038

Michael J. Pipas, Gary W. Witmer, and **Richard M. Engeman,** USDA/APHIS National Wildlife Research Center, Fort Collins, Colorado 80521-2154

Small Mammal Use of Hybrid Poplar Plantations Relative to Stand Age

Abstract

We studied small mammal use of a 9,300-ha complex of hybrid poplar plantations in northeastern Oregon from spring 1997 through winter 1999. Small mammals were surveyed in each of six plantation age classes four times per yr. A total of six rodent and one insectivore species were captured during the study. The three most common species, in declining order of abundance, were deer mouse, Great Basin pocket mouse, and house mouse. Small mammal abundance and species richness were greatest in 1- to 3-yr-old plantations and lowest in 4- to 6-yr-old plantations. Our study suggests that 1- to 3-yr-old hybrid poplar plantations provide suitable habitat for certain small mammals in this region, probably due to abundant understory vegetation. Once plantations reach 4 yr, canopy closure results in a relatively impoverished understory plant community, supporting fewer small mammal species at a lower abundance. Creating habitat heterogeneity by maintaining a diversity of plantation ages within the complex may enhance small mammal species diversity across these landscapes.

Introduction

The establishment of large, hybrid poplar (*Populus* spp.) plantations in North America is becoming increasingly popular with the forest products industry because of the ability of these fast-growing trees to produce abundant wood fiber in a short period of time. In the past 15 yr, over 28,000 ha of hybrid poplar plantations have been established in the Pacific Northwest to produce fiber for both paper and dimensional lumber products (Heilman et al. 1995). In addition to economic benefits, these plantations may provide environmental benefits such as erosion control and carbon sequestration (Paine et al. 1996, Isebrands 2000).

Little is known about the influence of these plantations on small mammal communities. Published studies of small mammal use of hybrid poplar plantations are few and relatively recent, and have taken place primarily in the Midwest (Christian et al. 1997, Christian et al. 1998). Furthermore, these studies primarily document wildlife use of plantations in comparison to surrounding land uses, rather than the effects of stand variables (e.g., stand age) on small mammal populations (Christian et al. 1997, 1998). Because of differences in understory plant cover that exist among different ages of hybrid poplar plantations in northeast Oregon, small mammal assemblages in different age classes may vary. In addition, the conversion of agriculture land and native habitat to plantations may affect both native and nonnative fauna by introducing exotic flora (Edge 2001, Witmer and Lewis 2001).

The current interest in hybrid poplar plantations, and the large potential land base available for plantations in North America (Graham 1994) necessitates an understanding of how small mammals use these plantations, because small mammals play an important role in ecological processes, including nutrient cycling, seed dispersal, herbivory, and predator-prey dynamics (Chew 1976, French et al. 1976, Potter 1976). The purpose of this study was to document small mammal use of hybrid poplar plantations in northeast Oregon. In addition, we hypothesized that small mammal relative abundance, species composition, and species richness would vary by plantation age.

Study Area

The study was conducted on a 9,300-ha complex of hybrid poplar plantations in the Columbia River Basin, Morrow County, Oregon. The natural vegetation in this region is steppe and shrub-steppe (Franklin and Dyrness 1988), and soil types are sandy and sandy loam. Topography varies from flat to slightly undulating with elevations ranging from 150 to 250 m. Annual precipitation averages 22 cm (Ruffner 1978), most of which falls in late winter and early spring.

Drip-irrigated plantations were first established in 1992, primarily on former agricultural crop-

[1] Author to whom correspondence should be addressed. E-mail: Brian.Moser@potlatchcorp.com

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lands irrigated by center-pivot systems. However, < 2 ha tracts of fallow vegetation were also converted to plantations when these tracts were adjacent to converted croplands. Plantations representing six age classes of trees (1- to 6-yr-old) were available for study. These variously aged plantations differed in both tree height and understory composition. On average, hybrid poplars in these plantations grew 3-5 m per yr. During the first 2-3 yr of growth, understory vegetation was often dense (> 90% cover). Common plant species present included the native horseweed (*Conyza canadensis*) and redroot pigweed (*Amaranthus palmeri*), and the naturalized Russian thistle (*Salsola kali*), tumble mustard (*Sisymbrium altissimum*), and cheatgrass (*Bromus tectorum*). Each plantation was sprayed with an herbicide-mixture of glyphosate and 2,4-D, and cultivated once during yr 1 and 2. However, most competing plants quickly recolonized given the favorable growing conditions. Complete canopy closure occurred following yr 3. At this point the understory became nearly devoid of live plants (< 5% cover) and was dominated by organic material primarily composed of leaf litter.

Methods

Three plantations in each of six age classes (1-, 2-, 3-, 4-, 5-, and 6-yr-old) were randomly selected from 229 available plantations to sample small mammal populations. Plantations studied ranged from 55 to 100 ha and all were planted during the first two weeks of April of each yr. Relative abundance and species composition of small mammals in each of the six plantation age classes were estimated by trapping with Sherman live traps (8 x 8 x 23 cm). A trapping grid of 49 traps (7 x 7 grid, 10-m spacing) was established at the center of each plantation. Pilot studies indicated that the appearance of new individuals and species dropped off markedly after four trap nights. Consequently, each replicate plantation was trapped for a period of four consecutive nights during each season (April-May 1997, July-August 1997, October-November 1997, January-February 1998, April-May 1998, July-August 1998, October-November 1998, and January-February 1999). Traps were baited with crimped oats and supplied with polyester batting for insulation. Traps were opened in the afternoon, checked in the morning, and closed during the day to reduce capture mortality. Each individual captured was identified to species, marked with ear tags or toe clipping, weighed, evaluated for breeding condition, and released at the capture site. Subsequent recaptures were not included in the analyses. Relative abundance was estimated as number of individuals captured per 100 trap nights. Mark-recapture analyses were not used because density estimates were not considered necessary to test the stated hypothesis. In addition, low capture rates encountered in some of the plantations would have produced unreliable density estimates using mark-recapture models (White et al. 1982).

Differences in combined relative abundance and species richness of small mammals among different plantation age classes were analyzed for each season using a one-way ANOVA, analyzed by the PROC MIXED procedure in SAS (Littell et al. 1996, SAS Institute Inc. 1996). A Fisher's protected LSD was used to isolate differences in means among age classes. Two-way ANOVA was used to analyze interactions between individual species and plantation age. Only the three most abundant small mammal species had sufficient capture data to provide meaningful individual analyses using the ANOVA procedure. Therefore, data from the four least abundant species were analyzed by the ANOVA procedures only as they could be pooled for overall small mammal abundance and species richness estimates. Differences were considered significantly different at $P = 0.05$.

Results

We captured 1,588 individuals of six rodent and one insectivore species during 28,224 trap nights over the eight trapping periods (Tables 1, 2). Captures included 1,230 (77.5%) deer mice (*Peromyscus maniculatus*), 143 (9.0%) Great Basin pocket mice (*Perognathus parvus*), 97 (6.1%) house mice (*Mus musculus*), 65 (4.1%) Merriam's shrews (*Sorex merriami*), 26 (1.6%) montane voles (*Microtus montanus*), 17 (1.1%) western harvest mice (*Reithrodontomys megalotis*), and 11 (0.7%) Ord's kangaroo rats (*Dipodomys ordii*).

Differences in small mammal species richness were detected among plantation ages during all trapping seasons, except summer 1997 and winter 1999. Species richness was always greater ($P < 0.021$) in 2-yr-old plantations when compared to 4- to 6-yr-old plantations, and was greater ($P < 0.012$) than 3-yr-old plantations during fall and winter 1998 (Tables 1, 2). Species richness in

TABLE 1. Mean species richness and small mammal captures per 100 trap nights on hybrid poplar plantations, 1997-1998. Means within a row followed by the same letter are not significantly different.

	Plantation Age					
	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6
			Spring 1997			
No. of species	1.0[a,b,c]	1.8[a]	1.5[a,b]	0.8[b,c]	0.3[c]	0.2[c]
No. of individuals	8.2[b]	17.5[a]	9.3[b]	1.0[c]	1.0[c]	0.2[c]
Deer mouse	2.5	8.7	6.8	0.5	0.5	0.2
Pocket mouse	5.7	2.7	1.3	0.2	0.0	0.0
House mouse	0.0	5.8	0.3	0.0	0.0	0.0
Harvest mouse	0.0	0.2	0.8	0.0	0.0	0.0
Montane vole	0.0	0.0	0.0	0.2	0.5	0.0
Kangaroo rat	0.0	0.2	0.0	0.0	0.0	0.0
Merriam's shrew	0.0	0.0	0.0	0.2	0.0	0.0
			Summer 1997			
No. of species	1.0[a]	1.5[a]	1.5[a]	0.7[a]	0.8[a]	0.5[a]
No. of individuals	2.5[b]	10.8[a]	11.2[a]	0.8[b]	3.5[b]	0.5[b]
Deer mouse	1.3	5.7	8.8	0.5	2.3	0.3
Pocket mouse	1.0	3.2	0.3	0.0	0.0	0.0
House mouse	0.2	1.8	0.8	0.0	0.0	0.0
Montane vole	0.0	0.0	0.7	0.0	0.7	0.0
Merriam's shrew	0.0	0.0	0.0	0.3	0.5	0.2
Harvest mouse	0.0	0.0	0.7	0.0	0.0	0.0
Kangaroo rat	0.0	0.2	0.0	0.0	0.0	0.0
			Fall 1997			
No. of species	0.7[a,b,c]	1.3[a]	0.8[a,b]	0.0[c]	0.3[b,c]	0.0[c]
No. of individuals	2.5[b]	8.0[a]	1.2[b]	0.0[b]	0.8[b]	0.0[b]
Deer mouse	1.3	6.2	0.5	0.0	0.0	0.0
Pocket mouse	1.2	1.3	0.0	0.0	0.0	0.0
Merriam's shrew	0.0	0.0	0.5	0.0	0.7	0.0
Montane vole	0.0	0.0	0.2	0.0	0.2	0.0
House mouse	0.0	0.3	0.0	0.0	0.0	0.0
Harvest mouse	0.0	0.2	0.0	0.0	0.0	0.0
			Winter 1998			
No. of species	1.3[a]	0.7[b]	0.2[c]	0.0[c]	0.2[c]	0.0[c]
No. of individuals	17.3[a]	16.8[a]	0.2[b]	0.0[b]	0.8[b]	0.0[b]
Deer mouse	16.5	16.5	0.0	0.0	0.0	0.0
Merriam's shrew	0.0	0.0	0.2	0.0	0.8	0.0
Harvest mouse	0.3	0.3	0.0	0.0	0.0	0.0
Pocket mouse	0.3	0.0	0.0	0.0	0.0	0.0
House mouse	0.2	0.0	0.0	0.0	0.0	0.0

1-yr-old plantations was greater ($P = 0.012$) than 3- to 6-yr-old plantations during fall 1998, and was greater ($P < 0.001$) than all other plantation ages during winter 1998 (Tables 1, 2). Species richness was greater ($P = 0.012$) in 3-yr-old plantations compared to 4- to 6-yr-old plantations during summer 1998, was greater ($P = 0.013$) than 5- and 6-yr-old plantations during spring 1997, and was greater ($P = 0.015$) than 4- and 6-yr-old plantations during fall 1997 (Tables 1, 2). Species richness was similar among 4- to 6-yr-old plantations during all seasons except spring 1998, when 6-yr-old plantations exceeded ($P = 0.021$) 4-yr-old plantations (Tables 1, 2).

Combined small mammal abundance differed among plantation ages during all trapping seasons except fall 1998. Total density was always greater ($P < 0.017$) in 2-yr-old plantations when compared to 4- to 6-yr-old plantations, was greater ($P < 0.017$) than 3-yr-old plantations during all seasons except summer 1997, and was greater ($P < 0.017$) than 1-yr-old plantations during all seasons

TABLE 2. Mean species richness and small mammal captures per 100 trap nights on hybrid poplar plantations, 1998-1999. Means within a row followed by the same letter are not significantly different.

	Plantation Age					
	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6
			Spring 1998			
No. of species	1.0[a,b,c]	1.7[a,b]	1.0[a,b,c]	0.3[a,b]	0.5[b,c]	1.2[a,b]
No. of individuals	8.8[b,c]	33.5[a]	13.2[b]	0.5[c]	1.2[c]	1.7[c]
Deer mouse	7.2	29.8	10.7	0.0	0.2	0.5
Pocket mouse	1.6	2.0	2.5	0.0	0.0	0.2
Merriam's shrew	0.0	0.0	0.0	0.3	1.0	0.8
House mouse	0.0	1.3	0.0	0.0	0.0	0.0
Montane vole	0.0	0.2	0.0	0.0	0.0	0.2
Harvest mouse	0.0	0.0	0.0	0.2	0.0	0.0
Kangaroo rat	0.0	0.2	0.0	0.0	0.0	0.0
			Summer 1998			
No. of species	1.0[a,b]	1.2[a]	1.2[a]	0.7[b,c]	0.3[c]	0.7[b,c]
No. of individuals	7.3[b,c]	17.3[a]	11.5[b]	1.7[c]	2.0[c]	4.7[c]
Deer mouse	6.5	16.0	10.5	1.5	0.8	3.2
House mouse	0.8	0.8	0.7	0.0	0.0	0.0
Merriam's shrew	0.0	0.0	0.3	0.0	1.2	0.3
Montane vole	0.0	0.2	0.0	0.0	0.0	1.2
Kangaroo rat	0.0	0.3	0.0	0.0	0.0	0.0
Harvest mouse	0.0	0.0	0.0	0.2	0.0	0.0
			Fall 1998			
No. of species	1.3[a]	1.3[a]	0.3[b]	0.3[b]	0.3[b]	0.3[b]
No. of individuals	7.5[a]	14.3[a]	1.8[a]	0.5[a]	0.2[a]	0.8[a]
Deer mouse	5.7	12.2	1.8	0.3	0.3	0.8
House mouse	1.3	1.5	0.0	0.0	0.0	0.0
Kangaroo rat	0.5	0.2	0.0	0.0	0.0	0.0
Montane vole	0.0	0.3	0.0	0.0	0.0	0.0
Merriam's shrew	0.0	0.0	0.0	0.2	0.0	0.0
Pocket mouse	0.0	0.2	0.0	0.0	0.0	0.0
			Winter 1999			
No. of species	1.0[a]	0.7[a]	0.3[a]	0.5[a]	0.5[a]	0.2[a]
No. of individuals	13.5[a]	4.8[b]	0.3[d]	2.8[c]	0.5[d]	0.2[d]
Deer mouse	13.0	4.5	0.0	0.0	0.3	0.2
Merriam's shrew	0.0	0.3	0.0	2.8	0.2	0.0
Pocket mouse	0.2	0.0	0.2	0.0	0.0	0.0
Kangaroo rat	0.3	0.0	0.0	0.0	0.0	0.0
House mouse	0.0	0.0	0.2	0.0	0.0	0.0

except winter 1998 (Tables 1, 2). Small mammal density was greater ($P < 0.017$) in 3-yr-old plantations compared to 4- to 6-yr-old plantations during spring and summer, and was similar during fall and winter (Tables 1, 2). Small mammal density was greater ($P < 0.009$) in 1-yr-old plantations compared to 4- to 6-yr-old plantations during spring 1997 and winter seasons. Total density was similar in 4- to 6-yr-old plantations for all seasons except winter 1999, when the density in 4-yr-old plantations exceeded ($P < 0.001$) 5- and 6-yr-old plantations (Tables 1, 2).

The deer mouse was the most abundant species captured in all plantation age classes combined (Tables 1, 2). The smallest effect was during fall 1997, when deer mouse captures outnumbered the pocket mouse by 3.3 times and the house mouse by 27 times ($P = 0.006$). The largest effect was during winter 1998 when the deer mouse was captured at a rate of 110 times greater ($P < 0.001$) than both the house mouse and pocket mouse. Densities for the pocket mouse and house mouse were similar during all trapping periods.

An interaction between plantation age and species abundance was detected ($P < 0.019$) during all trapping seasons except spring 1997 (Figure 1). Deer mouse densities typically peaked in 2-yr-old plantations and declined to near zero by age four. However, during winter 1999 the peak was in yr 1, in summer in yr 3 and in winter 1998 in yr 1 and 2. Pocket mouse and house mouse

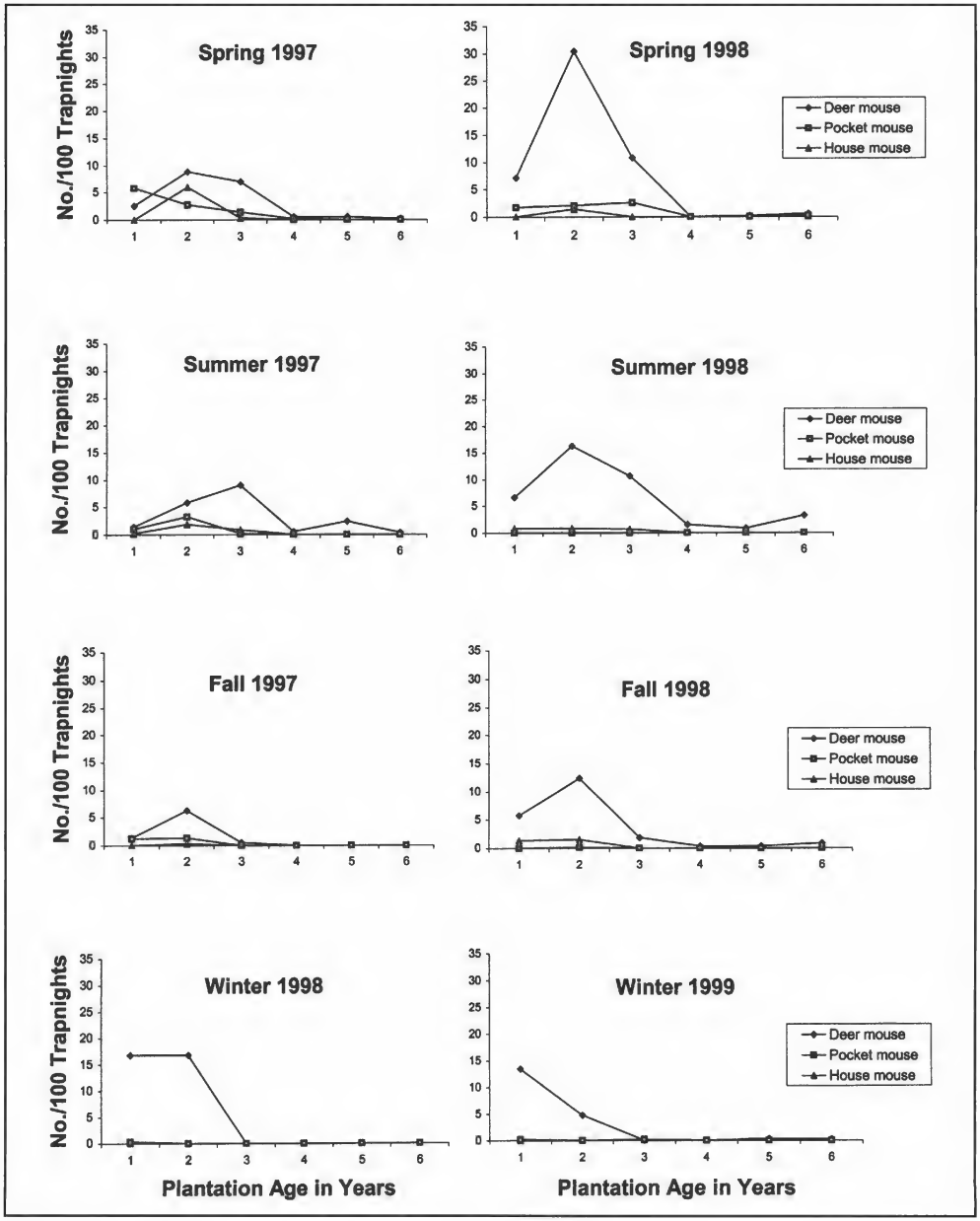

Figure 1. Change in rodent species abundance (number individuals per 100 trap nights) relative to stand age, spring 1997 through winter 1999.

densities peaked in 1- to 3-yr-old plantations, although the effects were not as large as for the deer mouse. Pocket mouse and house mouse densities declined to near zero by age four.

Discussion

High abundance and species richness of small mammals in young plantations were probably a result of abundant understory vegetation that provided both food and cover. Once plantations reached their fourth growing season, canopies closed and their floors were practically devoid of live plants, with abundant decomposing hybrid poplar leaves. Dyer et al. (1990) also reported that small mammal density was greatest in the youngest of short-rotation eucalyptus (*Eucalyptus camadulensis*) and casuarinas (*Casuarina cunninghamiana*) plantations in California, and gradually declined as the plantations aged. Total mammal densities were dominated by the deer mouse, which made up 77.5% of the total captures. The majority of captures in hybrid poplar plantations in the Midwest comprised habitat generalists, such as the deer mouse (Christian et al. 1997).

The only species captured consistently in the older plantations was Merriam's shrew, a species commonly associated with shrub-steppe (Hudson and Bacon 1956) and forest (Hoffmeister 1956). Thus, it was not surprising to find this species in the plantations, however, the insectivorous Merriam's shrews were captured only in the 3- to 6-yr-old plantations where the heavy leaf litter was abundant with attendant invertebrates such as worms and insect larvae. These small shrews were commonly observed moving below the leaf litter, which presumably provided cover from predators. The deer mouse commonly travels above this litter and is more susceptible to predation when herbaceous and woody cover is absent. Our results differed from Christian et al. (1997), who consistently captured other *Sorex* spp. in the young plantations that they studied.

A significant interaction between plantation age and species abundance demonstrated that species composition changed as plantations aged. The deer mouse was most abundant in 2-yr-old plantations, when vegetation control resulted in an early seral plant community preferred by the deer mouse (Borrecco et al. 1979). As plantations developed and the understory became less abundant, deer mouse numbers declined.

The pocket mouse was common in 1- to 3-yr-old plantations. Few were caught in winter, probably because the pocket mouse is torpid for > 90% of the winter months in this region (O'Farrell et al. 1975). The presence of the pocket mouse was most likely an artifact from the former shrub-steppe community and adjacent shrub-steppe areas. In addition, individuals might have immigrated into plantations from adjacent shrub-steppe. Verts and Carraway (1998) reviewed studies of the pocket mouse in Oregon and found it was most commonly associated with sandy soils in arid regions, dominated by shrub-steppe habitat. But the pocket mouse was also found in juniper woodlands in Oregon, which are structurally similar to shrub-steppe. Once our plantations reached 4-yr-old, the pocket mouse no longer inhabited them.

The house mouse was commonly captured in 1- to 3-yr-old plantations, but rarely in plantations > 4-yr-old. Again, lack of understory vegetation in older plantations created a hostile environment. True feral house mouse populations have not been reported previously in Oregon. Most of our plantations were > 0.8 km from human structures, suggesting young hybrid poplar plantations support feral populations. Dyer et al. (1990) also reported use of short-rotation plantations by the house mouse in California. Regardless of whether the house mouse dispersed from fabricated structures or persisted due to favorable habitat conditions, this mouse is an exotic species that may compete with native species or cause other adverse ecological consequences (Witmer and Lewis 2001).

Other species were low in abundance. The montane vole was captured in 2- to 6-yr-old plantations, and most of the sites within plantations where voles were caught had understory covers > 80% (even in the old plantations). Small patches of ground cover occur in old poplar plantations and provide refugia for small mammals in an otherwise inhospitable environment (Christian et al. 1998). The montane vole is economically important because it can cause irreparable damage to poplars by feeding on their bark and cambium (Moser and Witmer 2000). Vole populations can irrupt every 3-5 yr (Taitt and Krebs 1985), with high potential for tree damage. Another species captured only in plantations with higher-than-usual cover was the western harvest mouse. This species was captured in 1- to 4-yr-old plantations. Ord's kangaroo rat, a species commonly found

only in shrub-steppe, was captured only in 1- and 2-yr-old plantations. This species was probably an artifact of the original shrub-steppe (Rogers and Hedlund 1980). In addition, individuals might have immigrated into plantations from adjacent shrub-steppe.

Our study suggests that young hybrid poplar plantations that have not achieved canopy closure may contain relatively abundant and diverse populations of small mammals compared to older plantations. In addition, replacement of native shrub-steppe habitats with hybrid poplar plantations may still provide habitat for the first 3 yr for some small mammal species thought to be dependent on shrub-steppe habitats.

Although this study addressed large, commercial plantations, smaller plantings used as conservation plantings, windrows, and phytoremediation projects may contain higher densities of small mammals due to the increased edge effect. Because small mammals play an important role in ecological processes, including nutrient cycling, seed dispersal, herbivory, and predator-prey dynamics (Chew 1976, French et al. 1976, Potter 1976), it is important that land managers consider this faunal group when designing plantings.

Establishment of within-plantation heterogeneity by creating openings or planting different aged trees would further increase the suitability of these plantations for wildlife populations (Hanowski et al. 1997), including small mammals. However, designing plantations to increase biodiversity may reduce fiber yield and lead to an increase in densities of economically important species such as voles (*Microtus* spp.). Due to the potential of voles to cause severe damage to plantations (Moser and Witmer 2000), and the loss of fiber yield that results from such damage, it is likely that successfully managing hybrid poplar plantations for biodiversity by increasing within-plantation heterogeneity will remain a challenge for managers. If biodiversity is an important consideration when designing plantation landscapes, creating heterogeneity by maintaining a diversity of plantation ages within the complex may help ensure that the greatest diversity of small mammal species will occupy these landscapes.

Acknowledgments

Potlatch Corporation and Boise Cascade Corporation provided financial support and study sites. A. Mortensen and R. Reynolds provided valuable logistical support. We also thank G. Beauchamp for his valuable assistance with fieldwork. A. B. Carey, D. P. Christian, P. J. Heglund, and R. Morgan provided valuable reviews that improved the quality of this manuscript.

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Received 7 July 2001
Accepted for publication 6 October 2001

David J. Mattson,[1] U.S.G.S. Forest and Rangeland Ecosystem Science Center, Colorado Plateau Field Station, P.O. Box 5614, Northern Arizona University, Flagstaff, Arizona 86011-5614

Consumption of Wasps and Bees by Yellowstone Grizzly Bears

Abstract

I investigated the consumption of wasps and bees by grizzly bears in the Yellowstone region, 1977–1992, using data collected during a study of radio-marked bears. Although wasps and bees were not a major source of energy, Yellowstone grizzly bears are among only a few populations of their species in North America known to consume these insects in sometimes noteworthy amounts. Consumption of wasps and bees was greatest during the driest months of the study and during years when abundant ungulate carrion and few whitebark pine seeds were available. Peak consumption during dry years probably reflected increases in wasp and bee populations, whereas little consumption during years when pine seeds were abundant probably reflected a relative preference for pine seeds. The odds that bears would consume wasps and bees were greatest when they were in forest stands with abundant coarse woody debris and considerable live basal area. Excavation of ground nests also was most extensive in dense forest stands. All detected exploitation involved excavation of nests, almost all of which were located in or under logs and stumps or in duff near the base of trees. It is not clear if this pattern of exploitation reflected the distribution of wasps and bees, and, if so, why wasps and bees were concentrated in dense forests with abundant coarse woody debris. In short, Yellowstone grizzly bears apparently consumed wasps and bees most often when and where these insects were most abundant as well as when known high-quality bear foods were scarce.

Introduction

Consumption of wasps and bees (Hymenoptera: Vespidae and Apidae) by bears has hitherto received little scientific attention. However, even a casual survey of published research reveals that wasps and bees are part of the diets of black bears (*Ursus americanus* or *U. thibetanus*) and brown bears (*U. arctos*) throughout the northern hemisphere. In North America, consumption of wasps and bees by brown bears is relatively uncommon compared to consumption of these insects by black bears. Consumption was detected in only 6 of 21 brown bear diet studies versus 20 of 24 black bear diet studies compiled by Mattson (1998). Even so, consumption of wasps and bees by brown bears has been observed throughout brown bear range, including studies as far north as the southern Yukon (Pearson 1975) and central Alaska (Murie 1981) and as far south as central Montana (Aune and Kasworm 1989) and northwestern Wyoming (Craighead et al. 1995).

Details in the scientific literature about consumption of wasps and bees by bears are limited to anecdote and entries in tables summarizing bear diets. It is unclear whether wasps and bees are ever an important bear food and, if so, under what circumstances. Where feeding behaviors associated with consumption of native wasps and bees have been described, bears excavated these insects from subterranean nests (Sharafutdinov and Korotkov 1976, Slobodyan 1976, Lloyd 1979, Russell et al. 1979, Murie 1981, Servheen 1983, Cicnjak et al. 1987). In places like the Yellowstone region, at the current southern limit of North American brown bear range, most social ground-nesting species are wasps of the genus *Vespula*, most commonly *V. acadica*, *V. pensylvanica*, *V. vulgaris*, and *V. consobrina* (Evans 1970, Evans and Eberhard 1970, Akre et al. 1981). Unfortunately, little is known about ecological relations of these ground-nesting wasps, especially in boreal or high-elevation forested environments (Bohart and Bechtal 1957, Evans 1970, Evans and Eberhard 1970, Spradbery 1973, Akre et al. 1981).

Grizzly bears (*U. a. horribilis*) in the Yellowstone region are among the North American brown bears known to consume wasps and bees (Craighead et al. 1995). Yellowstone grizzly bears obtain most of their energy from whitebark pine (*Pinus albicaulis*) seeds and tissue from elk (*Cervus elaphus*) and bison (*Bos bison*)(Mattson et al. 1991). Most ungulate tissue is consumed by bears during April-May as carrion from animals that died of natural causes during the previous three months (Mattson 1997a). Whitebark pine seeds are consumed by bears primarily during September-October, from cones in ground-level caches

[1]E-mail: David_Mattson@usgs.gov

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made by red squirrels (*Tamiasciurus hudsonicus*) (Mattson et al. 2001). When pine seeds are abundant, the bears eat little else besides them (Mattson et al. 2001). During years when pine seeds and carrion are scarce, grizzly bears in this region eat diverse other foods, including insects such as ants (Mattson 2001).

In this paper I describe foraging on wasps and bees by grizzly bears in the Yellowstone region using data collected during a study of radio-marked bears from 1977–1992. My analysis was exploratory and designed to address the following questions: (1) How did the likelihood and level of consumption of wasps and bees by grizzly bears vary with season and monthly weather? (2) How did the likelihood of consumption vary with availability of known high-quality bears foods, specifically ungulate carrion and whitebark pine seeds? (3) How did likelihood and levels of consumption vary with site and vegetation features?

Methods

The approximately 23,000 km^2 study area, from 43°30' to 45°15'N latitude and from 109°30' to 111°30'W longitude, corresponded to the known range of Yellowstone's grizzly bear population. Most of the area occupied by grizzly bears is >2100 m in elevation and consists of remote mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Annual temperatures average about 0°C. Monthly averages during April through October range from –2°C to 13°C . Temperatures rarely exceed 27°C in most areas. Precipitation varies in amount and timing with elevation and region and falls mostly as snow that reaches accumulations of 20–260 cm, depending on location, before melting during March–June (Dirks and Martner 1982). About 75% of the study area was forested and most of this forest was dominated by lodgepole pine (*Pinus contorta*) (Despain 1990). Craighead et al. (1995) described the study area in detail.

Grizzly bears were trapped, marked, and radio-relocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). A subset of radio-relocations was visited and described according to methods described by Mattson (1997b, 2000). Field crews also described sites where grizzly bear feeding or bedding sign was encountered en route to and from telemetry locations. At each location, field crews established a variable-radius forest inventory plot (Avery and Burkhart 1994) at the center of grizzly bear activity. Trees were tallied, identified as live or dead, and the diameter of each was measured at 1.4 m aboveground. Additional information was collected within 10 m of plot center, including descriptions of coarse woody debris. These descriptions were indices of amount (1–7, none to heavy), size (1–7, small to large), and degree of decomposition (1–6, solid to well-decomposed). Based on double sampling, indices of size and amount were related to volume of woody debris, in kg m^{-2}, as follow: total volume = –0.0008 + 0.764ln(amount x size); r^2 = 0.75 (Mattson 1997b).

Field crews described all signs of feeding and collected all feces (scats) found at telemetry locations and elsewhere from 1977–1992. From 1986 to 1992, descriptions of feeding activity included measurements of excavations. For excavations of wasp and bee nests in duff or soil, length (*A*), width (*B*), and depth (*C*) were measured. Where a log or snag had been excavated, average diameter of the log where it was torn by the bear (*A*), total tear length (*B*), and average tear as a percent of total log circumference (*C*) were measured. Total excavated volume (in dm^3) was calculated as the product of $A \times B \times C$ for simple excavations and as $\pi\ (A/2)^2 \times B \times C$ for logs and snags (Elgmork and Unander 1998, Mattson 2001).

The concurrent collection of scats and information on feeding activity maximized comparability of data from these two sources at broad scales. I did not ascribe scat contents to specific feeding sites because foods found in scats were often not consumed at the site of collection given the 7–13 hr transit time of digesta (Pritchard and Robbins 1990). Thus, I compared data from scats and feeding sites by month but not by specific feeding sites. Scats were dried and analyzed for percent content according to methods described by Mattson et al. (1991). Results were reported by month and year as total frequency of occurrence in scats, percent of total fecal volume, and mean percent for scats in which the item occurred.

I used logistic regression analysis (Demaris 1992) to specify the effects of explanatory variables on the likelihood that a bear had or had not excavated wasp or bee nests at a given location. Radio-telemetry locations or feeding sites were units of analysis. I specified two models: one using

only data from telemetry locations, including sites where no feeding sign had been found, and the other using only data from sites with feeding sign, but including plots not at telemetry locations. I gave priority to the first model and used the second to confirm patterns. When wasps or bees had been excavated, I used multiple linear regression (Weisberg 1985) to specify the effects of explanatory variables on the total volume of excavations. I used maximum likelihood methods for parameter estimation and the sample-size-adjusted version of Akaike's Information Criterion (AIC_c) (Burnham and Anderson 1998) for model selection. I used change-in-AIC_c (Δ) to quantify the relative effect of each variable in a given model (Burnham and Anderson 1998). Because the value of AIC_c is affected by sample size, Δ is comparable within but not among models. I deemphasized statistical hypothesis testing for reasons well stated elsewhere (Johnson 1999) and I present *P*-values solely as confirmatory information.

I considered both proximal and distal effects in the analysis (Mattson 2000, Mattson 2001). Distal effects were those operational at broad temporal and spatial scales while proximal effects were operational at the scale of the immediate site. Proximal effects were represented by measures taken at telemetry locations or other sites of grizzly bear activity. Distal effects were enumerated from other sources, as follow. Numbers of ungulate carcasses on elk and bison winter ranges during spring and numbers of cones on whitebark pine trees were taken from counts at fixed transects. Monthly temperatures and precipitation were taken from regional summaries published by the U.S. National Oceanic and Atmospheric Administration (NOAA). I also used a running two-month sum of growing season (i.e., April–October) precipitation in the analysis. Mattson (2000) provided a more detailed description of these distal factors and their sources.

Results

During this study, 6662 scats were collected and 1853 telemetry locations of radio-marked bears were investigated to determine activity of the associated animal. Feeding sign was found at a total of 2769 sites, including sites not associated with a telemetry location. Remains of adult wasps or bees were found in 33 scats whereas sign of foraging for wasps or bees was found at 35 sites. No identifiable remains of wasp or bee larvae or pupae were detected in scats.

Grizzly bears consumed few wasps and bees in the Yellowstone region, generally <1% total scat volume (Figures 1a and 1b). However, use was greater during some years, as during 1988 when remains of wasps and bees accounted for 3% and 6% of total fecal volume during August and September. On average, levels of consumption and related foraging peaked during these two months (Figures 1a and 1b). I calculated the ratio of total volume of wasp or bee remains in fecal material to total volume of nest material exca-

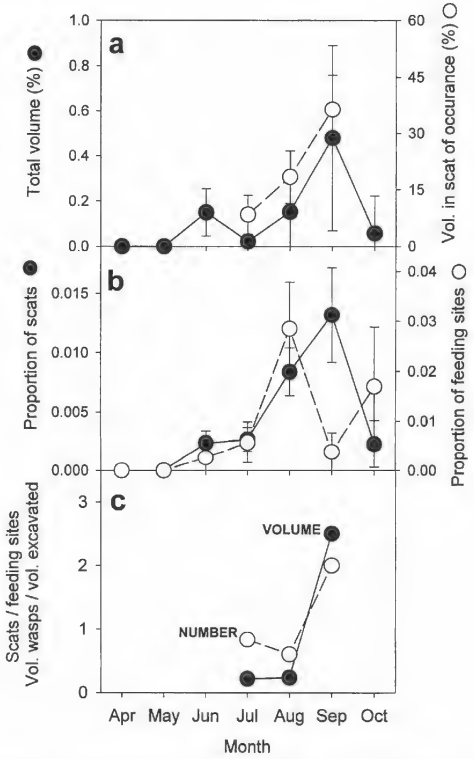

Figure 1. Monthly patterns associated with consumption of wasps and bees by Yellowstone grizzly bears, 1977–1992: (a) remains of wasps and bees as a percent of total fecal volume, averaged among years (± 1 SE), and as a percent of scats in which they were found, averaged among scats; (b) proportion of scats and feeding sites where the remains of wasps and bees or associated feeding sign were found; and (c) indices of reward obtained by consuming wasps or bees.

TABLE 1. Regression models for relations between either the logit-transformed probability that wasps or bees had been consumed, or the natural-log transformed volume of total excavations, and distal and proximal factors, for Yellowstone grizzly bears, 1977–1992. β is a parameter estimate and Δ is change in AIC_c with deletion of the corresponding variable from the model. Statistics for logistic regression models are for goodness-of-fit tests.

	Probability of consumption: Telemetry locations only			Probability of consumption: Feeding sites only			Volume of excavations (dm^3)[a]		
Independent variables	β	SE	Δ	β	SE	Δ	β	SE	Δ
Constant	–10.3	4.7		–9.8	3.4		2.5	0.58	
Distal factors									
Cumulative precipitation (cm)	–4.8[a]	1.2	39	–5.8[a]	1.1	88			
Number of ungulate carcasses	3.3[a]	1.6	9	3.7[a]	1.2	20			
Number of whitebark pine cones (n $tree^{-1}$)	–2.1[a]	0.9	8	–2.0[a]	0.7	11			
Proximal factors									
Total live forest basal area (m^2 ha^{-1})	1.02[a]	0.39	10	0.86[a]	0.24	16	0.067[c]	0.028	3.6
Amount of coarse woody debris (index)	0.038[b]	0.016	4	0.035[b]	0.013	5	–0.034[b]	0.011	0.1
Statistics									
G^2 or F (df)	76 (879)			117 (937)			6.4 (2 / 26)		
P	1.00			1.00			0.005		
R_L^2 or R^2	0.96			0.95			0.33		
n[d]	1556			2149			29		

[a]Coefficient was estimated for data transformed by: $\ln(x + 1)$.
[b]Coefficient was estimated for data transformed by: x^2.
[c]Coefficient was estimated for data transformed by: $(\ln[x + 1])^2$.
[d]Sample sizes used for modeling were less than total sample sizes because of missing values.

vated by bears, and the ratio of total number of scats with remains of these insects in them to total number of feeding sites where consumption was detected, to indicate the monthly level of energetic reward obtained by bears. Both indices peaked in September (Figure 1c), coincident with peak fractions of wasp and bee remains in scats where they were detected (Figure 1a). I did not calculate these indices for April–June or October because of few samples of scats ($n \leq 3$) and feeding sites ($n \leq 2$). There were 5, 12, and 12 feces containing the remains of wasps or bees collected during July, August, and September and 6, 20, and 6 sites with sign of feeding on these insects found during the same three months.

The probability that Yellowstone grizzly bears had consumed wasps or bees at a site, versus engaging in any other activity, was related to five factors considered in this analysis. Probability of consumption was more strongly related to proximal factors describing vegetation structure ($\Delta = 37$) than to distal factors related to weather and availability of known high quality foods ($\Delta = 20$). Of single factors, consumption was most strongly related to the sum of precipitation during the current and previous month, number of ungulate carcasses available on ungulate winter ranges during spring, and amount of live overstory basal area at the site (Table 1). The negative relation to precipitation was acute (Figure 2a); probability of consumption dropped sharply with increased moisture. Proximally, probability of consumption increased with increasing amounts of both coarse woody debris (deadfall) and live basal area (Figure 2b). When wasps or bees had been consumed, total volumes excavated by bears to reach nests also increased with increasing live basal area but declined with increasing amounts of woody debris (Table 1).

The gray remains of paper nests were observed at the center of grizzly bear excavations at 33 sites where consumption of wasps or bees was documented. Diameters of 14 nests sufficiently intact to measure averaged 1.1 ± 0.4 dm. Wasps, sometimes numerous, were observed in 30% of the 49 individual excavated nests. Of these nests, 26% were located partially in the base of stumps and snags, 22% were under logs, 17% were in logs, 17% were in forest duff <3 dm from the base of a tree, and 4% were in soil in the open.

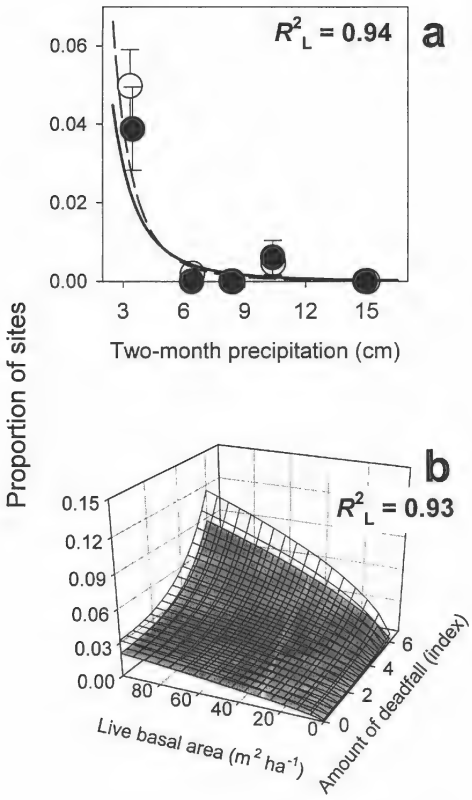

Figure 2. Relations between proportions of sites where wasps or bees had been consumed and (a) sum of precipitation during the current and previous month and (b) total live forest basal area and amount of coarse woody debris (deadfall). Filled circles and solid lines in (a) and the gray surface in (b) depict relations for telemetry locations only; open circles and dashed lines and the open mesh surface depict relations for all feeding sites. Circles denoting means and brackets denoting SEs are shown for quintiles of the data to illustrate goodness of fit; R^2 values are for relations based on telemetry locations.

Discussion

Peak consumption of wasps and bees by Yellowstone grizzly bears occurred late in the growing season, during August and September. This coincided with an apparent peak in the reward, or probable energetic benefit, of consuming these insects. A late season peak in relative abundance of wasps or bees, and related energetic benefit of use, is consistent with general trends in seasonal population dynamics of social ground-nesting wasps. Single queens usually start a colony in spring with numbers of adults, pupae, and nest combs peaking by August (Evans and Eberhard 1970, Spradbery 1973). Comparatively high levels of consumption by bears in September may reflect delayed phenology of colonies in the Yellowstone study area because of a climate colder here than where most investigations of wasp population dynamics have occurred.

Yellowstone grizzly bears consumed the most wasps and bees during the driest months of the entire study. This agrees with observations by Sharafutdinov and Korotkov (1976) who noted heavy consumption of ground-dwelling wasps by brown bears in the Ural Mountains during a year when wasp populations proliferated because of hot dry weather. Although research done elsewhere is equivocal about relations between weather and wasp abundance, there are some indications that dry weather promotes the growth of wasp populations (Spradbery 1973). I speculate that bears consumed wasps and bees more often during the driest months of the driest years simply because wasps and bees were then more abundant.

Consumption also increased when whitebark pine cone crops were small and ungulate carrion was abundant earlier in the year. As with ants (Mattson 2001), Yellowstone's grizzly bears probably consumed whitebark pine seeds in preference to wasps and bees. The positive association with availability of carrion during spring is not as easily explained. One speculative possibility is that growth of wasp populations was accelerated by availability and use of an energy-rich food (ungulate tissue) early in the growing season. Meat is readily consumed by wasps (Evans and Eberhard 1970, Spradbery 1973). Other explanations for this relation could involve changes in grizzly bear selection of foods like wasps and bees in response to availability of carrion and effects of weather correlated with over-winter mortality of ungulates.

The odds that Yellowstone grizzly bears consumed wasps and bees were greatest at sites with abundant deadfall and considerable basal area of live trees—conditions often associated with older forest stands (Romme 1982, Mattson 1997b). They also exploited more nests more thoroughly in dense forests, although not where deadfall was abundant. This association with live trees and woody debris is consistent with the frequent location of exploited wasp and bee nests in or under logs or

at the base of trees. Presumably, grizzly bears concentrated their foraging for wasps and bees in these kinds of sites because ground-nesting wasps were most abundant there. Even so, existing research gives no indication where wasps of boreal environments tend to nest, why this might be at sites where woody debris and live trees are more abundant, and, if so, how these stand features interact with effects of drought.

Although in North America wasps and bees are a common food of black bears, this is not the case for brown bears. Nowhere but in Yellowstone have North American brown bears been observed to consume wasps and bees more than a few times (Pearson 1975, Lloyd 1979, Russell et al. 1979, Murie 1981, Servheen 1983, Aune and Kasworm 1989). Yellowstone's grizzly bears are thus somewhat unusual among North American brown bears, not only in consuming these insects, but also by sometimes consuming noteworthy quantities of them. Even so, wasps and bees were not an important source of energy and nutrients for bears in this population during the study period, except during the extremely dry year of 1988 when regional precipitation during June–September was 39% of normal. As with many of Yellowstone's grizzly bear foods (Mattson et al. 1991), wasps and bees are potentially important to some bears at some times. This may become more common if regional precipitation diminishes as the global climate changes.

Acknowledgments

Many people contributed substantially to marking bears and collecting site data used for this analysis. Of those, a few deserve special recognition: S. Alt, D. Burrup, L. Cayot, D. Delsordo, D. Dunbar, G. Green, M. Haroldson, J. Henry, B. Hoskins, C. Hunt, J. Jonkel, K. Kendall, M. Knapp, J. Orpett, D. Reinhart, B. Schleyer, E. Shannahan, and R. Swalley. D. Stradley contributed the most of any to radio-tracking marked bears. R. Knight provided general supervision of this study. Data collection was funded by the U.S. National Park Service, Wyoming Game and Fish, U.S. Fish and Wildlife Service, and U.S. Forest Service. Completion of this analysis was supported by the U.S.G.S. Forest and Rangeland Ecosystem Science Center. I very much appreciate the generous support, monetary and otherwise, of M. Collopy and C. van Riper III of this bureau.

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Received 24 October 2000
Accepted for publication 3 November 2001

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Diana S. Sinton,[1] Division of Environmental Studies, Alfred University, Alfred, New York 14802

and

Julia A. Jones, Department of Geosciences, Oregon State University, Corvallis, Oregon 97333

Extreme Winds and Windthrow in the Western Columbia River Gorge

Abstract

Severe windthrow in the Bull Run watershed of the Oregon Cascade Range has occurred infrequently over the last 50 yr, yet individual storm events have generated extensive windthrow. In this case study, we consider two storm events known to have caused windthrow in the Bull Run. Using long-term meteorological records, we characterize the events and use the Gumbel extreme value distribution to analyze the wind speeds, estimating return intervals for the two storms. When all annual maximum wind speeds are considered for the 47-yr period of data, the 1973 and 1983 storm wind speeds may occur as frequently as every 5 yr or less, but this increases to a 10-15 yr interval when we analyze only east wind events. Extremely low air temperatures, characteristic of the storms, may have increased the likelihood of windthrow, though on at least one occasion a seemingly similar storm event failed to generate any windthrow. This exercise illustrates the complexity of natural disturbances such as windthrow and the inadequacy of simplistic, meteorologically-based models to predict a stochastic event accurately, particularly when natural patterns of windthrow are regularly altered by forest cutting.

Introduction

The Columbia River Gorge, cutting through the Cascade Range at the border of Oregon and Washington, is known for strong winds. Regionally, winter storms that develop over the Pacific Ocean are characterized by southwesterly winds. Less frequently, an easterly-wind storm pattern develops in response to a gradient between continental high pressure systems north and east of the Gorge and oceanic low pressure systems west of the Gorge (Cramer 1957). This phenomenon may be associated with a strong temperature gradient, especially when a continental high moves southward towards the Gorge from Canada and the Arctic. Strong easterly winds and low temperatures develop in the vicinity of the Gorge, which is the only near-sea level passage through the Cascade Range (Cameron 1931, Cameron and Carpenter 1936).

Windthrow, or the uprooting and snapping of trees by wind, is often associated with these high winds. Windthrow has occurred sporadically over the past century in the Bull Run watershed, a 265 km^2 basin located in the Mt. Hood National Forest, ~20 km south of the Columbia Gorge and west of Mt. Hood in north-central Oregon (Figure 1). Storms in 1973 and 1983, and several storms between 1890 and 1931, blew down a total of more than 10% of old-growth conifer stands in the Bull Run watershed (Sinton 1996).

Assessing windthrow risk is an important issue for forest management, ecology, and public safety in western forests. Windthrow has been associated with insect outbreaks, forest fires, and sedimentation of streams (Ruth and Yoder 1953, Gratkowski 1956, Franklin and Forman 1987, Agee 1993, Powers et al. 1999). Because the Bull Run watershed is the primary municipal water source for Portland, Oregon, extensive windthrow is a concern to the watershed's two managers, the city of Portland Water Bureau and the Mt. Hood National Forest.

The observed patterns of windthrow in the Bull Run have been linked to temporal changes in forest susceptibility, as happens when fresh edges are created by forest cutting (Franklin and Forman 1987, Sinton 1996, Sinton et al. 2000). An active timber harvesting program in the Bull Run was initiated by the U. S. Forest Service in 1958, and by the end of 1972, 10% of the forested part of the basin had been logged in scattered clearcut patches (Sinton 1996). Windthrow is commonly found at the edges of openings, such as clearcuts, and the windthrow in 1973 and 1983 displayed a strong spatial correlation with clearcut openings in the forest canopy (Franklin and Forman 1987,

[1] Author to whom correspondence should be addressed. E-mail: dsinton@alfred.edu

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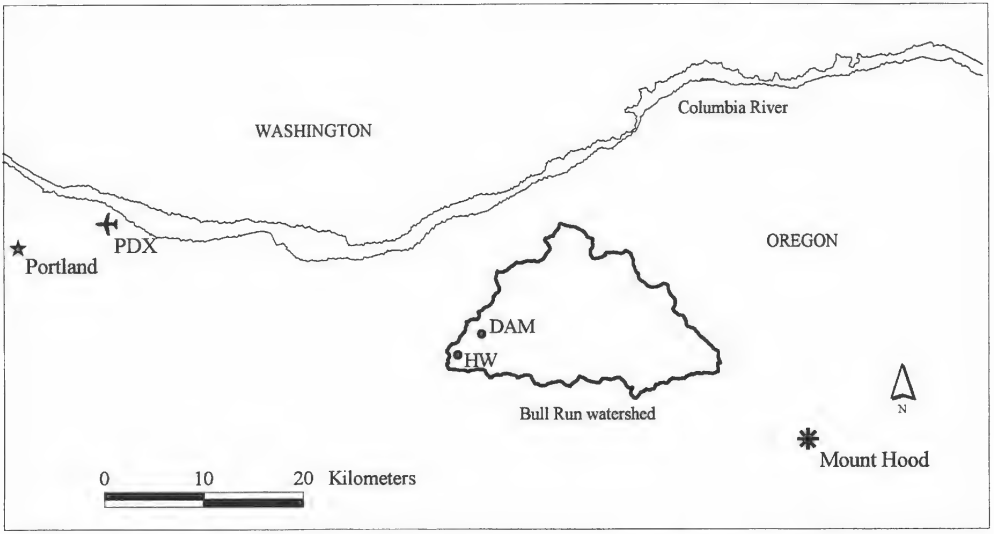

Figure 1. Bull Run watershed (Oregon), its vicinity, and climatic data collection sites. PDX = Portland Airport; HW = Headworks at Reservoir Two; DAM = Dam at Reservoir Two.

Sinton 1996, Sinton et al. 2000). In fact, much of the 1983 windthrow was contiguous to the salvage-related clearcuts that followed the 1973 storm event (Sinton 1996, Sinton et al. 2000).

The precise meteorological conditions contributing to windthrow at a site are rarely observed, making the prediction of windthrow from meteorological data a difficult task. Several windthrow studies suggest that the primary contributing climatic factors are high wind speeds and precipitation, leading to saturated soils that cannot firmly hold tree root systems (Day 1950, Fosberg 1986, Quine and White 1993, Stokes et al. 1995). However, it is not clear whether extreme gusts of wind are responsible for the damage, or sustained high winds over hours or days.

Furthermore, numerous non-meteorological factors contribute to windthrow, including individual tree or species characteristics, root decay, topography, and logging activities (Hubert 1918, Ruth and Yoder 1953, Gratkowski 1956, Fraser 1962, Stathers et al. 1994, Sinton et al. 2000). For example, during the Columbus Day Storm (12 October 1962), windthrow was extensive in the Pacific Northwest, particularly in the coastal regions (Lynott and Cramer 1966). On that day, Portland Airport recorded its highest wind speeds of the century (28.1 m/s), yet virtually no windthrow occurred in the Bull Run, the result of both its distance inland and a possible physiological resistance of the trees from chronic exposure to southwesterly winds (Sinton 1996).

Risk assessment may be performed by calculating a return interval for an event of a certain magnitude, estimating that the event has a certain probability of re-occurrence during that period (Gumbel 1958, Olsen et al. 1998). Using long-term records of wind speeds or stream flow, for example, we can then calculate a 100- or 500-yr event. In reality, an event of similar magnitude could occur multiple times or not at all during that time, as the event only occurs on average once during that period.

This case study identifies the meteorological conditions in the vicinity of the Columbia River Gorge that have been associated with windthrow in the Bull Run watershed. We describe two windthrow-generating storms (1973 and 1983) and consider the rarity of the storms' characteristics. We use a 47-yr record of annual maximum wind speeds to calculate a Gumbel reduced variate, a technique used to classify extreme events (Gumbel 1958), and compute return intervals for the two storm events.

Methods

Study Site

The temperature and precipitation regimes in the Bull Run watershed are typical of the Pacific Northwest: summers are warm and dry, and winters are cool and wet. Average annual precipitation in the Bull Run basin ranges from 2280 to 4300 mm, depending on elevation (Sinton 1996). Steep canyons and broad glacial valleys characterize the basin; 16% of the basin is ≤5° slope and 24% of the area is >20° slope. Elevation ranges from 225 m to over 1400 m, and 32% of the watershed is oriented towards the south and southwest. The primary vegetation is coniferous forest, composed principally of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), and western redcedar (*Thuja plicata*). Since 1958, about 17% of the basin has been clearcut; most of the remaining old-growth forest dates from a fire approximately 500 yr ago (Agee and Krusemark 2001).

Climatic Data Collection

We obtained meteorological data from a station located at the dam below Reservoir #2 in the Bull Run (DAM), the Headworks (HW) below this dam, and the Portland Airport (PDX), ~40 km to the west (Figure 1). We selected daily maximum and mean wind speeds, barometric pressure, wind directions, air temperature and precipitation amounts, because of their demonstrated association with windthrow events (Table 1) (Ruth and Yoder 1953, Gratkowski 1956, Quine and White 1993, Stathers et al. 1994). Long-term wind data were available only from PDX; wind speed correlations between PDX and DAM were strongest during east wind events in the winter months ($r = 0.47$) (Sinton 1996). Daily precipitation values measured at HW were also summed over a preceding 7-day period to create a variable indicative of antecedent soil moisture.

The Bull Run watershed has a moderate marine climate (Table 2). Measurable precipitation occurs on more than 60% of days throughout the year, but daily precipitation is moderate, with fewer than 5% of days receiving more than 2.5 cm of precipitation. Most mean and maximum daily wind speeds at the Portland Airport were low (Table 2). The highest daily mean wind speeds occur in winter, when winds from the east or southeast are more common, whereas low wind speeds characterize the summer months when winds are from the north and northwest. Winds came from the north, northeast, and east only 17% of the time, yet these wind directions are most associated with windthrow in the Bull Run (Sinton 1996).

Windthrow Data Collection

Documented windthrow was limited to events extensive enough to alter stand compositions, in patches greater than 0.56 ha, and be interpreted on aerial photographs (1:7920 or 1:12000, true color) (Sinton 1996). A mylar sheet marked with 0.6 cm^2 grid cells was placed over each photograph, and the presence of windthrown trees visible in any cell was noted. These data were entered into an ArcInfo (Version 6.0 and 7.01) geographic information system (GIS). Only two

TABLE 1. Climatic data collected in and around the Bull Run watershed, Oregon.

	Station Portland Airport (PDX)	Bull Run, Dam at Reservoir #2 (DAM)	Bull Run Headworks (HW)
Period of record	1948-1995	1993-1994	1931-1995
Data source	Oregon Climate Services (OCS)	OCS	OCS
Wind speed and direction			
hourly	X[a]	X[b]	
3-hourly	X[a]		
Daily barometric pressure	X		
Daily air temperature			X
Daily precipitation			X

[a] Wind speed observation frequency changed from hourly to 3-hourly at Portland Airport in 1985. The daily maximum wind represents an observed maximum gust within a one- or three-hour period, not a continuously measured variable or a fastest mile.

[b] Earlier records for the period 1978-1985 were not used because the data collected (rotations of device/day) were inconsistent with the other types of data.

TABLE 2. Characteristics of the climate around the Bull Run watershed, Oregon, 1948-1994. Precipitation and temperature data were recorded at HW; wind speeds and barometric pressure were recorded at PDX (see Figure 1). Variables are daily values, unless otherwise noted.

Descriptor	Precipitation (mm)	Precipitation (antecedent 7-days, mm)	Air temp. (maximum, °C)	Wind speed (mean, m/s)	Wind speed (maximum, m/s)	Barometric pressure (change from previous day, cm/Hg)
Minimum	0.0	0.0	-11.1	0.0	0.4	0.0
Maximum	172.7	365.5	41.1	15.2	22.8	0.78
Mean	5.6	39.2	16.1	3.7	6.3	0.11
Standard Error	0.08	0.31	0.06	0.01	0.02	0.001
Median	0.0	28.2	15.6	3.6	6.3	0.09
Mode	0.0	0.0	10.0	3.1	4.5	0.2
1st Percentile	0.0	0.0	0.6	0.0	2.2	0.001
5th Percentile	0.0	0.0	3.9	1.8	3.1	-0.23
95th Percentile	26.2	120.1	30.0	6.7	10.8	0.25
99th Percentile	46.7	176.5	33.9	8.5	13.4	0.4

such storm events (January 1973 and December 1983) overlapped with our period of wind data availability (1948-1994), and each of these triggered extensive salvage logging efforts (Sinton 1996).

Analytical Approach

We generated histograms and cumulative frequency distributions of the climatic data to characterize the climate of the Bull Run and describe the 1973 and 1983 storm events. We then used the maximum wind speeds per annum to generate Gumbel reduced variates to estimate the extremity of the wind speeds during the 1973 and 1983 storms. The Gumbel equation, also known as the Fisher-Tippett Type I, is commonly used for describing a generalized extreme value distribution with annual maxima data (Graham 1983), including events such as extreme stream and surge flows (Bardsley 1989, D'Onofrio et al. 1999), temperatures (Graham 1983), earthquakes (Dargahi-Noubary 1988) and wind speeds (Cook 1982, Revfeim and Hessell 1984, Linacre 1992, Galambos and Macri 1999, Brabson and Palutikof 2000). In our analysis, we further refined our characterization of the storm winds by recalculating the variate using only easterly maximum winds. With these techniques, we estimate return intervals for storms of similar magnitudes.

Results

Extremity of wind speeds

Gumbel variates and return intervals were calculated by using the annual maximum wind speeds during the 47-year-period of data from the Portland Airport (Table 3). Over two-thirds of these years had maximum winds from the south or southwest. With that data set, a wind speed of approximately 27 m/s would be a 100-year wind event, calculated with a Gumbel variate of 4.6 (-ln[-ln 0.99]) (Figure 2). Using annual maxima from all directions, the wind speeds from both the 1973 and 1983 storms have return intervals of <5 yr each.

Using only the highest annual easterly wind speeds to calculate Gumbel variates creates different return periods (Table 4). For winds from the east only, the 100-yr wind event would equal about 20 m/s (Figure 3). Based on these variates, the wind speeds recorded during the 1973 storm event would occur on average about every ten years, and the 1983 storm event was about a 15-yr wind event.

Storms in 1973 and 1983

Both the 8-9 January 1973 and 23-25 December 1983 storms were characterized by high maximum and mean daily wind speeds and maximum daily temperatures that failed to reach above freezing (Table 5). During both storms, the mean and maximum wind speeds were from the east and above the 99th percentile in their respective frequency distributions. This is consistent with the day-to-day barometric pressure changes of up to 0.3 cm/Hg, an amount that ranks in the 97th percentile (Table 5). Precipitation amounts were negligible in the 1973 storm, and during the 3-day

TABLE 3. Ranked wind speeds, return periods, and Gumbel reduced variates for all annual maximum winds from the Portland International Airport (PDX), 1948–1994. After Table 6.8 in Linacre (1992).

Annual maximum wind U: (m/s)	ln U	Number of values ≤ U[a]: m	100 C(U) percentile[b]	Exceedance 100 E(U)[c]	Return period[d]: T years	Gumbel reduced variate[e]
12.5	2.53	6	12.5	88	1.14	-0.73
13.0	2.56	7	14.6	85	1.17	-0.66
13.4	2.60	8	16.7	83	1.20	-0.58
14.3	2.66	13	27.1	73	1.37	-0.27
14.8	2.69	18	37.5	63	1.60	0.02
15.7	2.75	22	45.8	54	1.85	0.25
17.0	2.83	24	50.0	50	2.00	0.37
17.5	2.86	28	58.3	42	2.40	0.62
17.9	2.89	36	75.0	25	4.00	1.25
18.4	2.91	40	83.3	17	6.00	1.70
18.8	2.93	41	85.4	15	6.86	1.85
19.3	2.96	43	89.6	10	9.60	2.21
19.7	2.98	44	91.7	8	12.00	2.44
22.4	3.11	45	93.8	6	16.00	2.74
22.8	3.13	46	95.8	4	24.00	3.16
28.2	3.34	47	97.9	2	48.00	3.86

[a] m is the rank order of the value U
[b] i.e. 100 m / (N + 1), the number of values (N) being 47
[c] i.e. 100 – 100 C(U) per cent
[d] i.e. 1 / E(U), or (N + 1) / (N + 1 - m)
[e] –ln [-ln C(U)].

TABLE 4. Ranked wind speeds, return periods, and Gumbel reduced variates for the annual maximum easterly winds, Portland International Airport (PDX), Oregon, 1948–1994. After Table 6.8 in Linacre (1992).

Annual maximum wind U: (m/s)	ln U	Number of values ≤ U[a]: m	100 C(U) percentile[b]	Exceedance 100 E(U)[c]	Return period[d]: T years	Gumbel reduced variate[e]
9.9	2.29	1	2	98	1.02	-1.35
11.2	2.42	4	8	92	1.09	-0.91
11.6	2.46	5	10	90	1.12	-0.82
12.1	2.49	8	17	83	1.20	-0.58
12.5	2.53	18	38	63	1.60	0.02
13.0	2.56	19	40	60	1.66	0.08
13.4	2.60	26	54	46	2.18	0.49
13.9	2.63	29	60	40	2.53	0.69
14.3	2.66	36	75	25	4.00	1.25
14.8	2.69	39	81	19	5.33	1.57
15.7	2.75	42	88	13	8.00	2.01
17.0	2.83	43	90	10	9.60	2.21
17.5	2.86	44	92	8	12.00	2.44
17.9	2.89	46	96	4	24.00	3.16
18.4	2.91	47	98	2	48.00	3.86

[a] m is the rank order of the value U
[b] i.e. 100 m / (N + 1), the number of values (N) being 47
[c] i.e. 100 – 100 C(U) per cent
[d] i.e. 1 / E(U), or (N + 1) / (N + 1 - m);
[e] -ln [-ln C(U)].

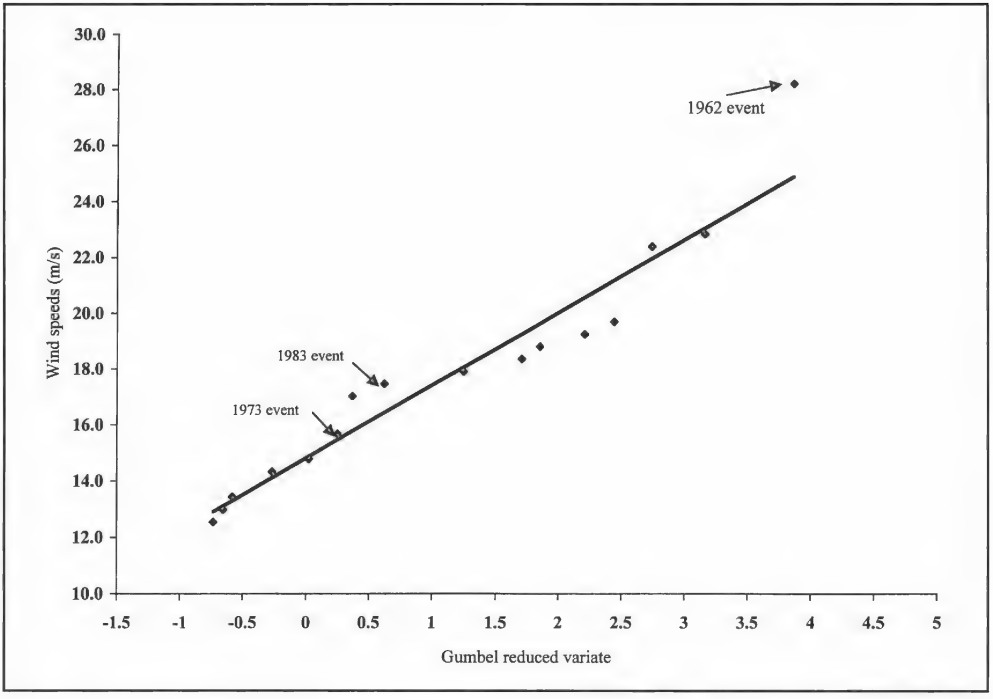

Figure 2. Plot of the Gumbel reduced variate against annual maximum wind speed at PDX (see Table 4).

TABLE 5. Meteorological characteristics of the January 1973 and December 1983 wind storms. Wind speed and barometric pressure data are from Portland International Airport (PDX), Oregon. Temperature and precipitation data are from the Headworks (HW) Station within the Bull Run watershed, Oregon.

Variable	8-Jan-73	9-Jan-73	23-Dec-83	24-Dec-83	25-Dec-83
Mean wind speed (m/s)	12.5	13.9	10.8	15.2	10.8
Maximum wind speed (m/s)	13.9	15.7	15.7	17.5	14.8
Direction of maximum wind	east	east	east	east	east
Change in barometric pressure from previous day (cm/Hg)	-0.21	-0.54	0.02	-0.81	-0.78
Maximum temperature (°C)	-3.3	-0.6	-7.2	-7.8	-0.6
Mean maximum temperature or preceeding two days (°C)	-1.9	-3.3	-6.9	-7.5	-7.5
Precipitation (mm)	0.0	0.0	0.0	2.3	5.3
Precipitation total from previous seven days (mm)	26.2	7.6	7.9	10.2	11.9

1983 event, the precipitation amounts ranked in the 70th percentile or below.

The combination of high easterly wind and low air temperatures occurs infrequently in the Bull Run. There were only 18 days during the years 1948-1994 when both the mean and maximum wind speeds were in the top 1% of their frequency distribution, and maximum air temperatures were in the lowest 1% of their distribution (Table 6). When we group consecutive days into storm events,

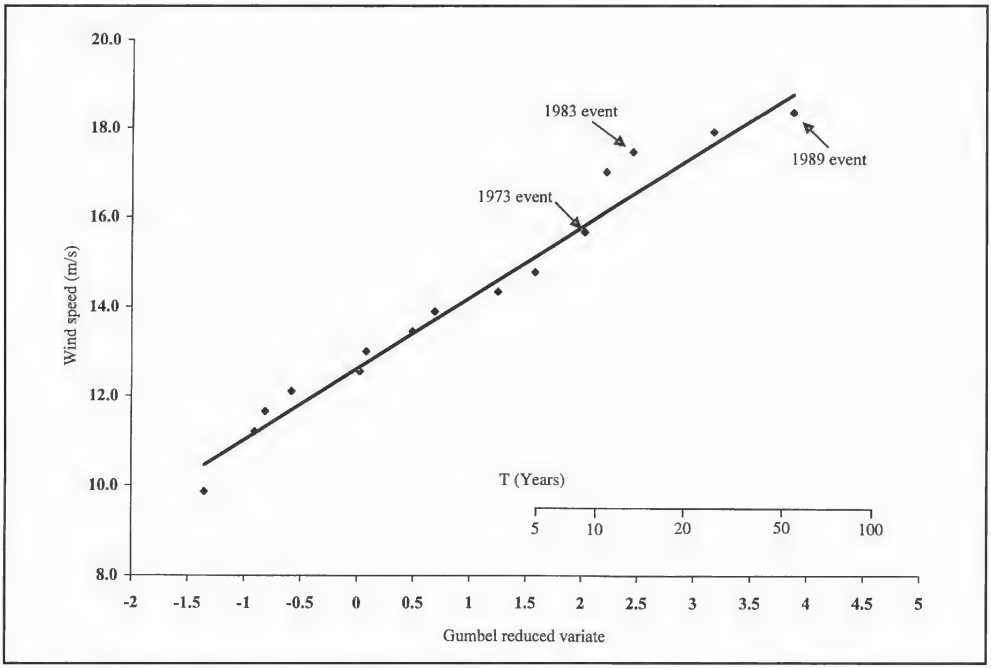

Figure 3. Plot of the Gumbel reduced variate against annual maximum easterly wind speed at PDX (see Table 5). Return intervals for selected years and associated wind speeds are shown on the graph.

TABLE 6. Individual and consecutive days when easterly wind and temperature conditions are within the top 1% of their frequency distribution, 1948-1994. Wind speeds are from PDX and temperature data are from HW. Dates when windthrow is known to have occurred in the Bull Run are highlighted in bold.

Dates	Mean wind speeds (m/s)	Maximum wind speed (m/s)	Direction of max winds	Maximum air temp. (°C)	Maximum air temp. on preceding 2 days (°C)
20-Jan-60	12.1	14.3	east	1	1
03-Mar-60	9.4	14.3	east	0	6
12-Jan-62	10.8	14.3	east	-3	4
19-Dec-64	9.0	13.4	east	1	-2
05-Dec-72	10.3	17.9	east	-3	5
06-Dec-72	9.9	14.3	east	1	-2
08-Jan-73	**12.5**	**13.9**	**east**	**-4**	**-1**
09-Jan-73	**13.9**	**15.7**	**east**	**-1**	**-4**
02-Jan-74	9.0	14.3	east	0	4
04-Jan-79	13.0	14.3	east	1	-1
05-Jan-79	12.1	14.3	east	-1	1
23-Dec-83	**10.8**	**15.7**	**east**	**-7**	**-6**
24-Dec-83	**15.2**	**17.5**	**east**	**-8**	**-7**
25-Dec-83	**10.8**	**14.8**	**east**	**-1**	**-7**
02-Feb-89	13.4	14.4	east	-2	10
03-Feb-89	15.2	18.6	east	-11	2
04-Feb-89	9.0	10.8	east	-4	-2
07-Jan-93	10.4	14.9	east	1	3
08-Jan-93	8.7	11.2	east	0	1

we find that windthrow occurred in the Bull Run on two out of six, 2- or 3-day storms.

Discussion

The easterly winds that generated extensive Bull Run windthrow were not particularly rare or infrequent ones. Meteorological controls on windthrow may be obscured by low spatial and temporal resolution of available data, and because reliable long-term wind records were available only at a site about 40 km from the basin. Accurate prediction of windthrow in the Bull Run would benefit from reliable local wind speed monitoring, rather than extrapolation from a distant site. During the 1983 event, the wind-monitoring device at HW ceased to function on the second day of the storm, so estimating the extremity of local winds was impossible. Furthermore, windthrow may be produced by the highest wind speed sustained for one or two minutes, rather than an arbitrarily selected five- to ten-minute sampling period once an hour, but only recently have wind data at Portland Airport begun to be collected as such fine temporal resolution.

Understanding the infrequent combination of high, easterly winds and sub-freezing temperatures may be critical for windthrow prediction in the Bull Run. Ice-loading in tree canopies has been suggested as a factor contributing to the 1983 Bull Run windthrow (Nancy Diaz and Ivars Steinblums, Mt. Hood National Forest, personal communication), and the conditions existed to create rime ice, formed when fog or other moisture-laden air is blown against a cold surface. While little precipitation was measured during either the 1973 or 1983 storm event itself, fog is a common characteristic of the Bull Run watershed (Harr 1982).

A Gumbel distribution of extreme values can be affected by the nature of the data set. The Gumbel method is designed for use with monthly or annual maxima, with at least a 20-yr-period of data availability (Tabony 1983, Linacre 1992). Brabson and Palutikof (2000) found that their wind speed data fit the Generalized Extreme Value (GEV) (i.e. Gumbel) distribution poorly, while Galambos and Macri (1999) found the Gumbel distribution a good match with their wind data. Mitsiopoulos et al. (1991) evaluated several distributions and found that Gumbel had rates of estimated error similar to or better than the normal, Weibul, and lognormal distributions. The particularly strong linear relationship found with the easterly wind data (Figure 3) suggests that the Gumbel distribution approximates the PDX data set well.

Restricting the Gumbel distribution to only easterly winds was an appropriate step for the Bull Run, but would not be suitable for other sites in the region. Given the prevailing southwesterly winter storm pattern in the Pacific Northwest, windthrow in the region is typically generated from southwesterly storms, particularly along the Coast (Gratkowski 1956, Fredriksen 1965). However, all of the windthrow observed in the Bull Run watershed during the 20th century has been generated by northeast- and east-wind events, with downed trees lying towards the southwest (Sinton 1996), and throughout the western half of the Columbia River Gorge, tree morphology indicated that trees were more frequently affected by easterly winds (Lawrence 1939).

Monitored meteorological conditions alone do not adequately explain the observed patterns of windthrow in the Bull Run. Observed windthrow in 1973 and 1983 was spatially associated with both ephemeral and perennial openings in the forest canopy (Sinton 1996, Sinton et al. 2000). On the other hand, a severe storm of two days duration occurred in February 1989 (Figure 3), with easterly winds of 18.4 m/s, approximating a 50-yr storm event. Although new fresh forest edges had been created by recent salvage of 1983 windthrow, and air temperatures during this event were also low (Table 6), no measurable windthrow was detected in the Bull Run (Sinton 1996). Vulnerable trees along openings may have 1) already been removed by earlier storms; 2) been pruned by other winds and thus had low risk of windthrow; or 3) produced adaptive growth to accommodate an additional wind load (Telewski 1995).

Nevertheless, the lack of windthrow associated with the 1989 storm supports our understanding that meteorological information alone is insufficient to predict windthrow. Topographic, edaphic, and vegetative factors must be considered in each individual case. Windthrow over the past few decades in the Bull Run represents an interaction between two dynamic patterns, the spatial pattern of forest fragmentation and the temporal pattern of infrequent, severe east wind events. While the combination of low air temperatures and high, easterly wind speeds is relatively

uncommon, a similar event in the future could still put Bull Run trees at risk for windthrow.

Acknowledgements

This research was supported by a cooperative agreement between the Mt. Hood National Forest, the City of Portland Bureau of Water Works, the Pacific Northwest Research Station of the US Forest Service, and Oregon State University (No. PNW 92-0220) and by NSF grant DEB-96-32921 (H.J. Andrews Long-term Ecological Research [LTER]). Climate data from Oregon Climate Services courtesy of G. Taylor. Discussions with and reviews by F. Swanson, D. Robbins, F. Sanders, D. Greenland, and two anonymous reviewers, improved the study.

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Received 17 May 2001
Accepted for publication 4 January 2002

Northwest Science Notes

The purpose of "Notes" is to publish short papers (typically less than five pages in length). There is no specific format or content required for articles published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

Sally A. Simmons and **William H. Rickard,** Washington State University, 2710 University Drive, Richland, Washington 99352

Demise of an Isolated Buckwheat Stand by Repetitive Wildfires

Abstract

Wildfires burned across permanently-marked study plots placed in a low elevation, small, isolated rock buckwheat stand three times between 1983 and 2001. With the passage of each wildfire, the number of buckwheat shrubs diminished until there were no living shrubs. Self-recovery of buckwheat by natural seed dispersal will likely be a slow process.

Introduction

Rock buckwheat (*Eriogonum sphaerocephalum*) occurs on stony ridge crests scattered throughout the semi-arid interior Columbia River Basin of eastern Washington (Daubenmire 1970). Sandberg's bluegrass (*Poa secunda*), a small perennial grass, characteristically dominates the sparse understory, making buckwheat stands somewhat resistant to wildfire compared to stands of big sagebrush (*Artemisia tridentata*) growing on normal soils that typically support cheatgrass (*Bromus tectorum*) or bluebunch wheatgrass (*Pseudoroegneria spicata*) as understory dominants. Buckwheat stands tend to be isolated from neighboring stands. Buckwheat does not readily sprout after burning thus wildfires are a significant threat. Fire may also encourage the spread of alien invasives such as cheatgrass that further encourages the ignition and spread of fire (Soll et al. 1999). This work describes the impact of repetitive burnings on rock buckwheat shrubs on the Arid Lands Ecology (ALE) Reserve, a 30,000 ha research natural area located in the Rattlesnake Hills 26 km northwest of Richland in Benton County, Washington.

Methods

Buckwheat density was determined by counting individual shrubs rooted inside four 3 m x 15 m (45 m^2) plots distributed across a 1 ha rock buckwheat stand at 180 m elevation on the ALE Reserve. Shrubs were counted in 1983, 1985, 1986, 1988, and 2001. Canopy cover of shrubs and herbs was ocularly estimated on ten 0.5 m x 1.0 m microplots spaced at 3-m intervals along a 30-m tape line in this same stand in April 2000 and in spring 2001. The stand was burned by a massive wildfire ignited by an automobile accident in late June 2000. Previous wildfires were ignited by lightning strikes.

Results

In 1983, mean rock buckwheat density was 60 shrubs per 45 m^2 (Table 1). After burning in 1984, shrub density was reduced to 21 and 22 in the first and second growing seasons. A second wildfire in 1987 burned through the same study plots and shrub density in the 1988 growing season was 3.2 shrubs per 45 m^2. A third fire burned in summer 2000 and in the 2001 growing season there were no surviving rock buckwheat shrubs.

Canopy cover of 13 species of herbs and shrubs measured in the spring of 2000 before burning averaged 54%, of which 13% was contributed by rock buckwheat (Table 2). In 2001, only five species were recorded in the same

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TABLE 1. Mean density and range of values of living rock buckwheat shrubs in permanently-marked plots in the year before and after three burnings between the years 1983 and 2001 (after Rickard 1989).

Year	Status	Mean density/45m^2	Range
1983	Pre-burn	60	48-77
1984	Burned		
1985	Burned +1	21	12-37
1986	Burned +2	22	12-42
1987	Burned		
1988	Burned +1	3.2	1-5
2000	Burned		
2001	Burned +1	0	0

TABLE 2. Mean canopy cover (%) by species at a rock buckwheat stand on the ALE Reserve in south-central Washington in April 2000 and 2001 before and after passage of wildfire.

	2000	2001
Perennials	Pre-burn	Post-burn
Eriogonum sphaerocephalum	13	0
Poa secunda	29	17
Lomatium gormanii	0.5	0.9
Erigeron poliospermus	0.2	0
Lomatium macrocarpum	0.1	0.1
Annuals		
Bromus tectorum (A)	8.7	4.3
Draba verna	1.0	0.2
Sisymbrium altissimum (A)	0.9	0
Holosteum umbellatum (A)	0.4	0
Microsteris gracilis	0.2	0
Plectritis macrocera	0.1	0
Epilobium paniculatum	0.02	0
Descurainia pinnata	0.02	0
Total Cover	54	23
# of Species	13	5
# of Annuals	8	2
# of Perennials	4	3

(A) = Alien invasives

plots and contributed a total canopy cover of only 23%. Six of the eight species not found in 2001 were annuals. None of the buckwheat shrubs survived the fire (Table 2).

Discussion

Rocky ridge crests occupy relatively little of the total area of ALE, but they contribute greatly to species richness. Most of the buckwheat stands are located along ridge crests at elevations between 400 and 1000 m above sea level. These high elevation crests support perennials not found at the low elevations, e.g. thyme buckwheat (*Eriogonum thymoides*), rosy balsamroot (*Balsamorhiza rosea*), narrowleaf goldenweed (*Haplopappus stenophyllus*), desert yellow daisy (*Erigeron linearis*), and Hood's phlox (*Phlox hoodii*). Two permanently-marked study plots had been established at higher elevation ridge crests prior to the 2000 wildfire, but these plots were not burned. After three burnings, the low elevation stand that we studied has not been aggressively invaded by cheatgrass and supports native Sandberg's bluegrass as the understory dominant with cheatgrass, spring whitlowgrass (*Draba verna*), and two species of desertparsley (*Lomatium* spp.) as subordinates (Table 2).

A better understanding of the long-term impact of wildfire on rock outcrop plant communities will require systematic monitoring of a number of permanently-marked study plots at various elevations and information on all species including non-vascular plants.

Acknowledgements

This work was supported in part by the Pacific Northwest National Laboratory's Office of Fellowship Programs under U. S. Department of Energy contract number DE-AC06-76RLO (1830).

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Received 13 November 2001
Accepted for publication 29 December 2001

Donald F. McAlpine,[1] New Brunswick Museum, 277 Douglas Avenue, Saint John, New Brunswick, Canada E2K 1E5

Stan A. Orchard,[2] and **Kelly A. Sendall,** Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, Canada V8W 9W2

Recent Occurrences of the Green Turtle from British Columbia Waters

Abstract

Seven recent occurrences of the green turtle from British Columbia waters are documented. There are only two previous reports of this sea turtle from the province. Records of fresh carcasses or live green turtles off British Columbia have been collected during the September- December period, outside the July–October turtle season for the northeastern Pacific. Based on carapace lengths, British Columbia occurrences appear to involve large juvenile and small adult turtles. Data on thermal tolerance in cheloniid turtles suggest that this species cannot survive for extended periods in British Columbia coastal waters. Although green turtle presence off British Columbia appears to be accidental, there is need for an organized effort to assess sea turtle status in British Columbia waters.

Introduction

There are only two previously published records for the green turtle (*Chelonia mydas*) from British Columbia waters. An 11.8 kg green turtle, with a 47.6 cm carapace, was found near the high-tide mark at Springs Cove at the entrance to Ucluelet Inlet, Vancouver Island (48° 57'N 125°33'W) on 6 December 1954 (Carl 1955). Although alive when discovered, the turtle later died and is now housed in the collection of the Royal British Columbia Museum (RBCM 908.00). Gregory and Campbell (1984) state that this turtle was probably just off course. Hodge and Wing (2000) list repeated sightings of a live green turtle off Dundas Island in September 1981 (54°50'N 130°67'W). In the course of preparing a review of the status and conservation of marine turtles in Canadian waters we encountered seven additional recent occurrences of the green turtle off British Columbia. Here we document and discuss these new green turtle observations. The only other sea turtle species recorded off British Columbia is the very distinctive leatherback (*Dermochelys coriacea)* of which there are 22 documented reports, mostly of live animals. Recent records for the olive ridley sea turtle (*Lepidochelys olivacea)* and the loggerhead sea turtle (*Caretta caretta)* from Washington and Alaska suggest these turtles may be recorded as accidentals off British Columbia in the future (McAlpine et al. 2002).

Recent Occurrences

The seven new records are summarized in Table 1. Several of these are supported by photographs and in one case, specimen material. Correspondence, and photographs additional to those presented here, relating to these records have been archived in the RBCM and the New Brunswick Museum. Photo-identifications were confirmed following reference to Márquez (1990) and Pritchard and Mortimer (1999).

On 25 April 1994 a green turtle carcass washed ashore at Schooner Cove, Pacific Rim National Park, Vancouver Island (Rod Palm, Tofino, B.C. personal communication). The four, non-overlapping, lateral scutes characteristic of the green turtle are visible in Figure 1. We have contacted the respondents who observed green turtles reported by Ebbesmeyer (2000) in the Beachcomber's Alert Newsletter. Judith Perris (Ucluelet, B.C. personal communication) discovered a single green turtle carcass on 28 February 1997 along the west central coast of the Ucluth Peninsula, Vancouver Island. Rodney Schatz (Masset, B.C. personal communication) has confirmed that he observed four green turtle carcasses in the Queen Charlotte Islands during 1999-2000. Two turtles beached on 9 November and 16 November 1999. Again, the four, non-overlapping, lateral scutes characteristic of the green turtle are visible in photographs of these turtles (Figures 2 and 3). Both turtles were

[1]Author to whom correspondence should be addressed. E-mail: dmcalpin@nb.aibn.com

[2]Current address: World Wide Fund for Nature, GPO Box 528, Sydney, NSW 2001, Australia.

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TABLE 1. New records for the green turtle from British Columbia.

Date	Location	Latitude/Longitude	Carapace Length	Remarks
25 April 1994	Schooner Cove, Pacific Rim National Park	49° 04'N 125° 48'W	~60 cm	decomposed carcass
9 November 1995	5 km south of Rose Point, Graham Island	54° 12'N 131°38'W	71 cm	fresh carcass
28 February 1997	Ucluth Peninsula, Vancouver Island	48°57'N 125°35'W	~100 cm	carcass
16 November 1999	Fife Point, Graham Island	54° 06'N 131°40'W	81 cm	fresh carcass
Late November 1999	East coast Graham Island	~ 54°01'N 131°43'W	81 cm	carcass
January 2000	East coast Graham Island	~ 54°01'N 131°43'W	unknown	carcass
28 January 2000	Metchosin, Vancouver Island	48° 26'N 123°28'W	87 cm	carcass

observed along the east coast of Graham Island, the first about 5 km south of Rose Spit, the second at Fife Point. Turtles were fresh dead when discovered and the observer felt the first turtle may have been alive when initially beached. The two remaining green turtles were also discovered in the same area, between Rose Spit and 32 km south, one in late November 1999, the other in the first week of January 2000. On 28 January 2000 a decomposed female green turtle estimated to weigh 45 kg washed ashore at Metchosin, Esquimalt Lagoon, Vancouver Island. The stranding was reported in the local newspaper (Curtis 2000) on 29 January and the skeleton has been added to the RBCM collection (catalogue number 1935.00). Although it was not possible to determine cause of death for this animal, a necropsy revealed a rolled piece of clear plastic wedged in the pylorus, possibly causing partial or intermittent obstruction (Helen Schwantje, DVM, Postmortem report on Green Sea Turtle, RBCM files).

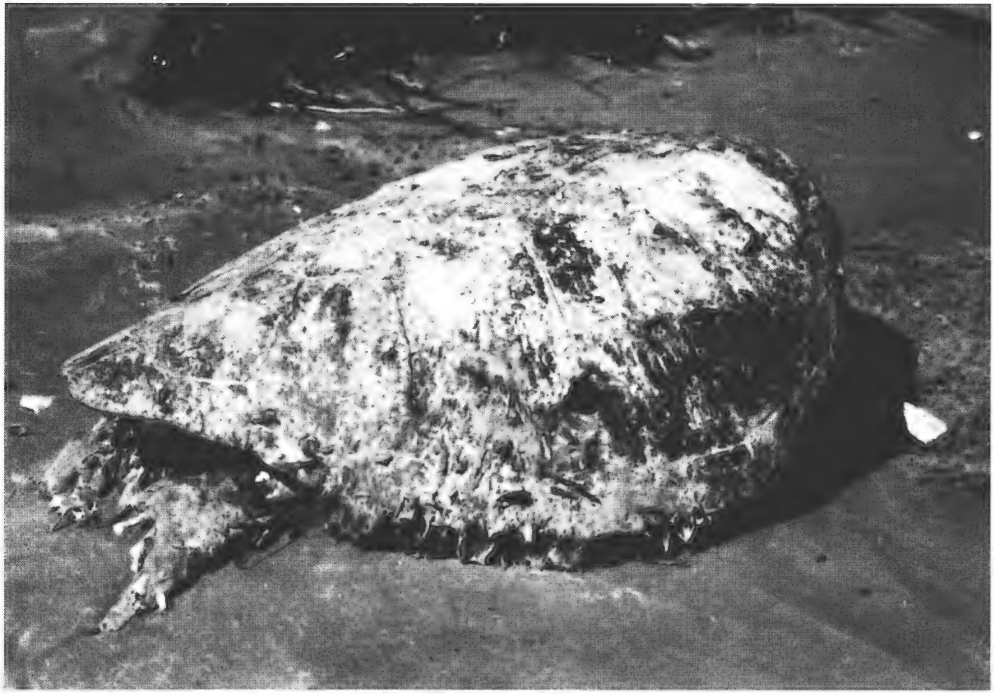

Figure 1. Decomposed carcass of a 60 cm carapace length green turtle washed ashore in Pacific Rim National Park, British Columbia on 25 April 1994 (R. Palm photo)

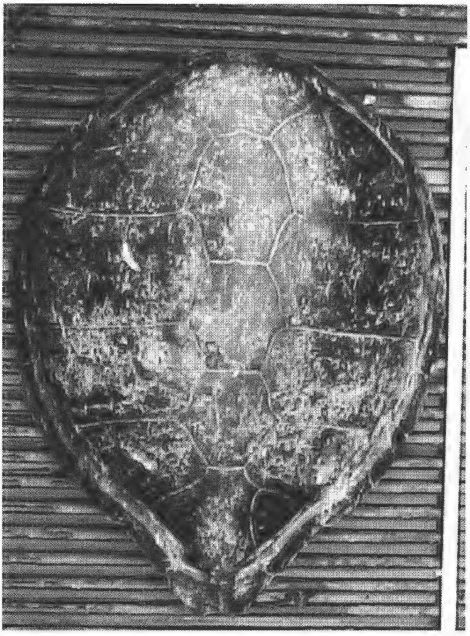

Figure 2. Carapace of a fresh 71 cm green turtle carcass washed ashore near Rose Spit, Graham Island, British Columbia on 9 November 1999. (R. Schatz photo)

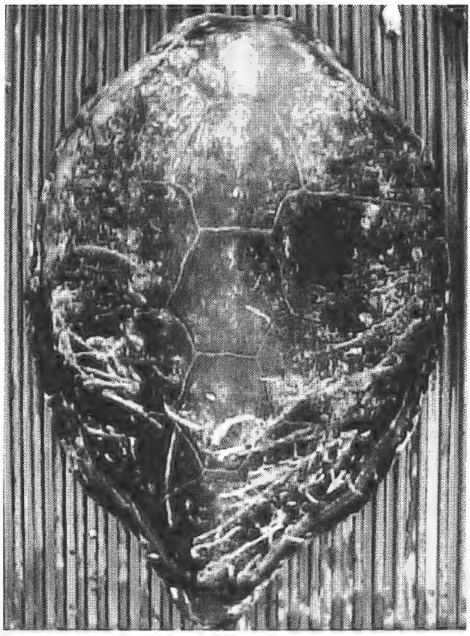

Figure 3. Carapace of a fresh 81 cm green turtle carcass washed ashore at Fife Point, Graham Island, British Columbia on 16 November 1999. (R. Schatz photo)

Discussion

British Columbia records of live green turtles or carcasses known to be fresh have been made during the September-December period (Table1; Carl 1955, Hodge and Wing 2000). All of these records are outside the July–October turtle season for the northeast Pacific (Hodge and Wing 2000). Recorded carapace lengths range from 47.6–87.0 cm.

Although size at sexual maturity in the green turtle varies between the sexes and among populations (Ernst et al. 1994), British Columbia records appear to involve large juvenile and small adult turtles. Cheloniid turtles are very close to their minimum thermal tolerance when they enter inshore Canadian waters, suggesting that the green turtle cannot survive for extended periods in coastal British Columbia (Schwartz 1978, Birse and Davenport 1987, Davenport 1997). On the basis of the single live green turtle recorded from British Columbia at that time, Gregory and Campbell (1984) suggested that this species should be considered accidental in the province. The current few reports of live green turtles in British Columbia waters subsequent to 1955 support this opinion. However, Hodge and Wing (2000) consider that sea turtles are too frequent in Alaskan waters to be an accidental part of the marine fauna. On the basis of four live sightings and four carcasses they list green turtles as rare. Although sea turtles appear to be less common off western than eastern Canada (McAlpine et al. 2002), the few British Columbia records in the literature probably under-represent the number of sea turtles entering British Columbia waters. An organized effort to assess sea turtle status off British Columbia is needed.

Acknowledgments

We are especially grateful to respondents Rod Palmer, Judith Perris, and Rodney Schatz for providing details concerning their observations. Dr. Curtis Ebbesmeyer was also helpful in putting us

in contact with observers and checking the records of the Beachcombers' and Oceanographers' International Association. David Fraser, British Columbia Fish And Wildlife Branch kindly assisted us in locating a news clipping relating to one of the January 2000 reports.

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Received 10 September 2001
Accepted for publication 3 January 2002

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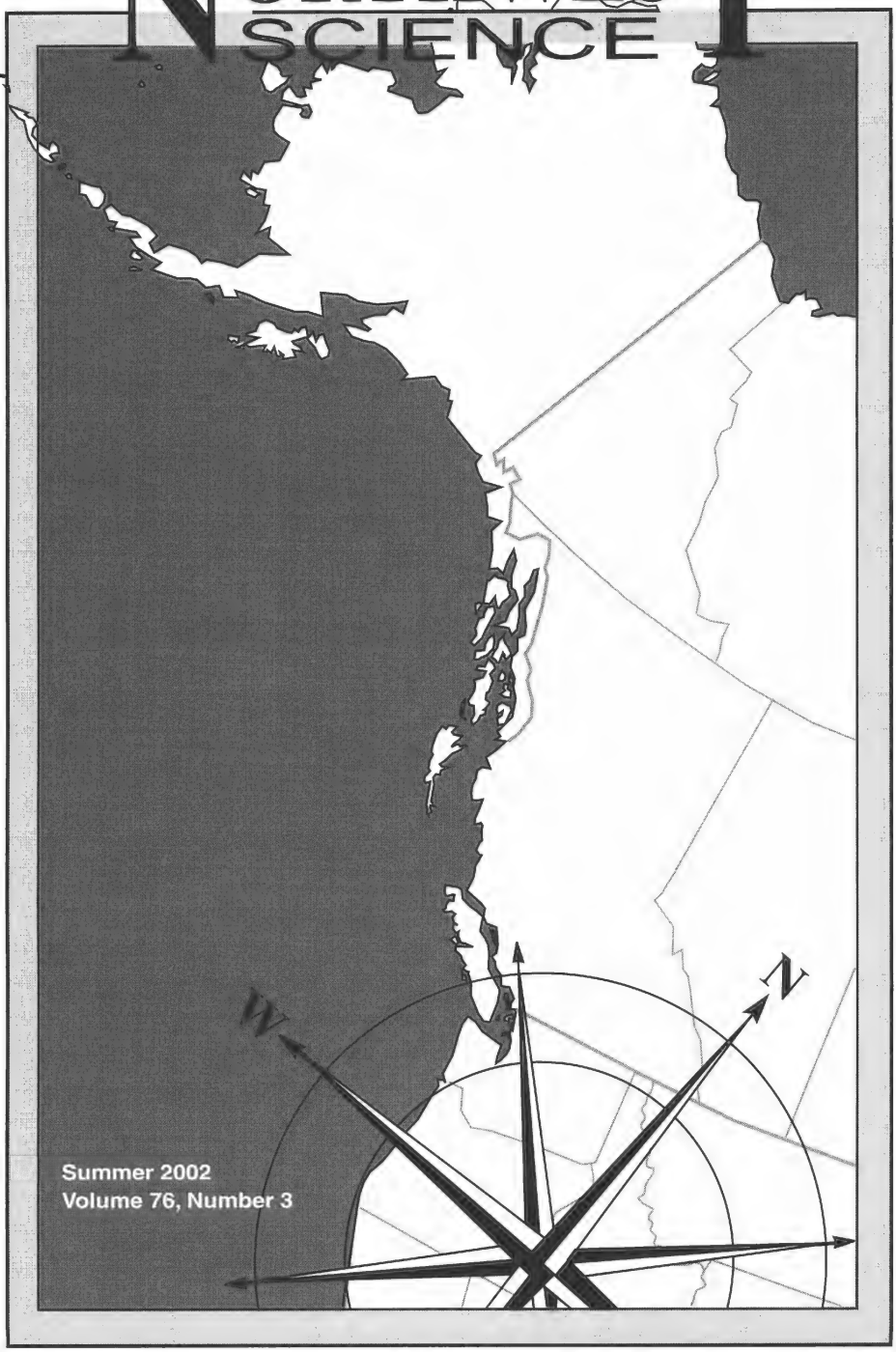

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Information for Authors

David Peter[1] and **Constance Harrington,** Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, Washington 98512-9193

Site and Tree Factors in Oregon White Oak Acorn Production in Western Washington and Oregon

Abstract

Acorn production in Oregon white oak is variable and not well understood. To determine tree, stand, and environmental characteristics influencing acorn production, we surveyed 284 trees in September and October 1999. Surveyed trees extended from Whidbey Island, Washington, to Roseburg, Oregon, and ranged in age from 11 to over 300 yr. Acorn production was ranked on a 1-4 scale (nonproducing to heavily producing), and tree size, condition, site, stand, and vegetation characteristics were recorded. All acorns were counted on 18 trees. Acorn production started around 20 yr and plateaued around 80 yr. Trees with inverted vase-shaped crowns typical of dense forest stands produced fewer acorns than those with columnar- or mushroom-shaped crowns typical of more open areas. Open-grown trees growing in well-drained, loamy soils had the highest productivity within natural settings. Trees in urban parks with fertilization or irrigation also produced well. Trees underburned 6-10 yr before the survey produced better than trees not underburned or trees underburned more recently. Trees growing in slough-sedge wetlands, steep south-facing rocky balds, or with unhealthy crowns produced the least. Understanding the factors that influence production of Oregon white oak acorns could help managers increase acorn crop size as many of the factors can be altered by management activities.

Introduction

Relatively little is known about the reproductive potential, silviculture, or ecology of Oregon white oak (*Quercus garryana*), a widely distributed western North American species (Stein 1990). Little is known about Oregon white oak reproduction in general, and acorn production in particular, even though acorns are a rich source of food for many mammals, birds, and insects (Barrett 1979, Ryan and Carey 1995a). The age when a tree first bears fruit, the age of maximum production, and the average quantity of acorns produced have not been determined (Stein 1990). Information is needed on the regularity of flowering and the variability within and between stands and locations (Stein 1990). It is not known if acorn crop variation is primarily controlled by variation in flower production, or success of flowering and fruit production.

The range of Oregon white oak extends from halfway up the eastern side of Vancouver Island, Canada, south through the Puget-Willamette Trough in Washington and Oregon, into northern California to the vicinity of San Francisco. A shrubby variety extends south along the western Sierra Nevada foothills to northern Los Angeles County. The easternmost extension of the range occurs north and south of The Dalles, Oregon in Kickitat County, Washington, and Wasco County, Oregon. Data for this paper were collected from almost half the range of the tree form of the species (Figure 1).

Oregon white oak produces heavy seed crops on an irregular basis and acorns mature from September to November (Stein 1990). Anecdotal information for Oregon white oak suggests heavy seed-crop years are followed by one or more years of poor productivity, and that good and bad years are somewhat synchronized over broad geographic areas. Variation in production from year to year, species to species, and tree-to-tree can vary greatly for oak species (Koenig 1980).

Oregon white oak has been diminishing over its natural range since the beginning of Euro-American settlement (Reed and Sugihara 1987, Agee 1993, Bell and Papanikolas 1997). Conversion to agriculture, urban areas, and other forest types (intentionally or through natural succession) are the major reasons for loss of oak stands (Ewing 1997). Remaining oak stands are now changing rapidly due to introduction of exotic species, overtopping by conifers, and fire exclusion (Chappell and Crawford 1997, Tveten and Fonda 1999).

Western gray squirrels (*Sciurus griseus*) in Washington maintain populations only where

[1]Author to whom correspondence should be addressed. E-Mail: dpeter@fs.fed.us

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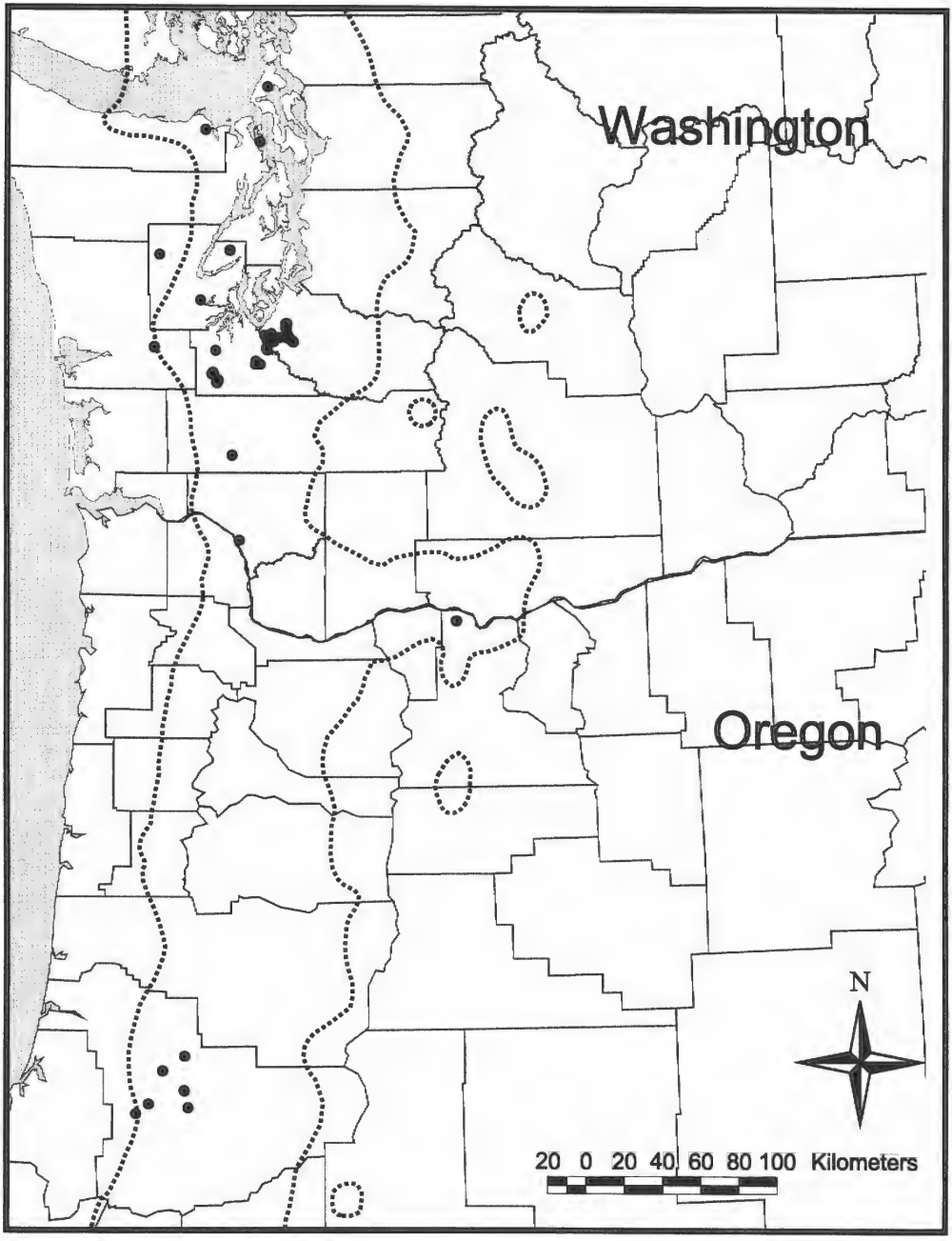

Figure 1. 1999 Oregon white oak acorn sampling sites in Washington and Oregon. Dashed line shows the range of Oregon white oak (Little 1971).

Oregon white oak communities exist (Roderick 1987). Acorns are critical fall and winter food for this squirrel (Steinecker and Browning 1970). One of the greatest threats to the western gray squirrel (threatened in Washington) at Fort Lewis, Washington, was Oregon white oak habitat loss due to succession and invasion of Douglas-fir (Ryan and Carey 1995b).

Recent public interest in Oregon white oak systems has focused new attention on how they can be managed and regenerated. We hope to provide new insights to aid managers in establishment of new oak stands, regeneration of existing oak stands and management of wildlife that utilize or depend on acorns. Specifically we asked how competition affects acorn productivity, how such competition can be recognized, what are the most important physical environmental variables for acorn production, and how past fire affects acorn production?

Methods

Surveys were conducted from 26 August to 14 October, 1999 before acorn drop. Data were collected by personnel from the United States Forest Service Pacific Northwest Research Station (PNW). Natural resource management professionals, amateur botanists from native plant society chapters, and forestry graduate students also volunteered to collect data. Volunteers obtained data forms and instructions by contacting the Olympia Forestry Sciences Lab or by downloading them from the project website. Oregon trees were sampled by volunteers who received only web-based instruction. Washington trees were sampled by PNW crew members or trained volunteers. Tree age, height, crown shape, and stand basal area were collected only on trees sampled by PNW personnel.

Acorn surveys were completed on 284 trees from 60 sites in 9 geographic areas. The PNW team sampled 153 Oregon white oak trees in Washington from Whidbey Island in the north to near Longview in the south. Volunteers contributed data for an additional 131 trees from the south Puget Sound area, a site near Mosier, Oregon, and from several sites near Roseburg, Oregon (Figure 1). Only acorns on the tree or healthy, ripe acorns that fell late in the survey period were considered (Table 1).

TABLE 1. Abbreviated method for classification of acorn abundance (Graves, 1980).

- Acorns should be mature—yellow-green to brown
- If acorns are not readily observed, the tree is either a Class 1 (nonproducing) or 2 (light producing). No acorns = Class 1. One or more acorns = Class 2.
- If acorns are readily observed, the tree is either a Class 3 (medium producing) or 4 (high producing). The tree is Class 3 if acorns are readily visible all around the tree and borne predominantly singly. The tree is also Class 3 if the acorns are only on one side, but are numerous or borne in multiples. A Class 4 tree is characterized by clusters of two or more acorns, all around the tree. The limbs often bend from the weight of acorns.

Characteristics of Sites

Sample sites were selected to represent the range of oak habitats, but a larger sample was obtained from more common habitats. Oak sites were selected across a continuum from slough-sedge wetlands to steep, dry, south-facing rock outcrops. Sites included agricultural, urban, and natural settings. Natural settings included savannas, forest edge, and oak or mixed oak-conifer forests. The largest sample (173) was from natural settings on relatively flat, extremely well-drained Spanaway soils in the south Puget Sound area, which is the most common oak habitat in western Washington. We deliberately selected several sites that had been prescribed burned in the last 10 yr to allow us to examine the effects of fire on acorn production.

Site data included percent of ground disturbance under the canopy, principal understory species, land use, water availability, and whether the tree had been fertilized in the past according to the landowner. The PNW team and some volunteers collected additional data on elevation, aspect, percent slope, years since last fire, soil series, understory species lists, and percent canopy coverage for grass, forbs, shrubs, trees, and bare ground. Missing elevation and aspect data were obtained from digital elevation models or USGS topographic maps.

For general descriptive purposes, data were averaged by nine geographic areas, chosen to represent specific populations or distinctive environments: Douglas County, Oregon; Wasco County, Oregon; Lower Columbia River, Washington; Lewis County, Washington; Lower Chehalis River,

TABLE 2. Sample size and mean site and stand characteristics by geographic area. The sites are in Washington unless otherwise noted.

Geographic area	n	Elevation (m)	Slope (%)	BH age[1] (years)	Height (m)	Crown width (m)	Breast height diameter (cm)	Basal area m^2/ha	Crown contact (%)
Douglas Co., OR	30	228	8	-	17	8	68	-	32
Wasco Co., OR	5	416	28	-	8	7	34	-	27
Lower Columbia River	5	10	9	129	22	12	66	15	65
Lewis County	2	139	3	123	22	19	108	4	25
Lower Chehalis River	5	3	0	139	18	15	73	20	42
South Puget Sound	62	67	4	83	15	9	41	11	43
Fort Lewis	154	99	5	70	12	8	37	12	38
South Fork Skokomish	6	434	88	144	5	4	20	15	23
Northern Puget Sound	15	31	12	77	14	10	53	12	52

[1]Breast-height age (1.3 m).

Washington; south Puget Sound, Washington; Fort Lewis, Washington; South Fork Skokomish River, Washington; and Northern Puget Sound, Washington. Fort Lewis is a subset of the south Puget Sound, Washington, area that we recognized as a separate unit because the sampling density in that area was much greater than elsewhere.

Mean elevation of all 60 sites in 9 geographic areas ranged from 3 m to 434 m above sea level (Table 2). The lowest elevation sampled was 2 m at Oak Bay in northern Puget Sound and the highest elevation was 463 m near the South Fork of the Skokomish River, which is a tributary to Hood Canal in western Washington. Most trees were on gentle topography. The sample was heavily weighted toward savanna and forest settings, although 19 trees were in urban settings and 15 in agricultural settings. Eight trees in city parks were irrigated, 18 were adjacent to wetlands, and 5 were in wetlands.

Moisture

To examine the relationship of moisture availability to acorn production we looked at available water content of the soil and precipitation. Soil series was assigned to tree locations using appropriate soil survey maps and field notes. This was done by overlaying field-mapped or GPS locations with soil series maps in ArcView®, or by locating mapped sites on USDA Soil Conservation Service county soil survey maps. Field notes were used to select the soil series from the list of possible soils in soil mapping unit descriptions, and available water capacity (AWC) data were obtained for each soil series in the sample from the MUIR database (USDA, NRCS 1994). Total available water capacity (AWC = cm of water per cm of soil by soil layer) was calculated by summing the total available water in each layer in the top 150 cm of soil. Annual precipitation (cm) for each site was obtained from PRISM maps (USDA, NRCS, and OSU 1999). A simple moisture index was calculated by multiplying the AWC by the annual precipitation and dividing by 100. The scale at which these soil moisture and precipitation data are mapped make them inappropriate to use for analyses at the individual tree level, but we believe they are adequate for stand or regional averages as we have used them.

Characteristics of Trees

At each site 1-11 trees (mean = 4) at least 1.3 m tall were selected. Trees were selected without regard to numbers of acorns, shape, crown contact, health, age, or size. Data collected for all trees included diameter at 1.3 m above ground (breast height), acorn class, percent crown contact with other trees, and health class. Percent crown contact was defined as the percent of the sample tree's crown circumference that is merged with other tree crowns of similar or greater stature. Percent crown contact is a measure of the competitive environment around the sample tree.

Additional data collected by PNW personnel included tree height, crown width, crown class, height to live crown, crown shape, and basal area

around each tree. Basal area around the sample tree is a measure of competition. We used calibrated angle prisms on variable radius plots to determine basal area (Bell and Dillworth 1997). Basal area was taken at a point 1 m north of the base of the bole and did not include the sample tree. Crown width was measured at the long axis of the crown and an axis at right angles and averaged. Height to live crown was measured as the mean height from the ground to the lower tips of the foliage. Crowns were classed as mushroom, columnar, or vase shaped (Figure 2).

Acorn Abundance

All surveyors ranked acorn abundance on a 1-4 scale (nonproducing to heavily producing) (Graves 1980). Table 1 gives an abbreviated account of the method, but the full method was used to train surveyors. This method is a simple repeatable procedure that works well with minimally trained observers. Graves (1980) found that three observers gave the same classification to 74% of the trees, and that in the remaining 26% of the trees two of the three observers agreed. He showed a relationship between this method and the more quantitative seed trap method. There was a positive correlation between acorn abundance class and acorns collected per seed trap and significant differences between classes 2, 3, and 4 (light, medium, and heavy) for both trap sample weight and number of acorns per trap sample (Graves 1980). PNW crew members cross-checked during training were consistent in producing the correct class. Volunteers who received PNW instruction in the method have consistently been able to give the same results as the PNW trainer. Volunteers who first learned the method from the web site and were later checked by PNW crew members have also been consistently correct. This method works well with minimally trained volunteers because the classes are broad.

The PNW team also counted all the acorns in a subsample of trees. Eighteen trees were carefully inspected and acorns counted by one of two methods. Four trees were counted from a lift truck with a 15-m boom, which produced highly accurate counts. Fourteen trees were counted from the ground with binoculars. All counted trees were first classed using the abundance scale (Table 1). Trees were measured, photographed, and the shapes were sketched. External surface area of the crown shape was calculated to permit calculation of acorns/m^2 of external crown surface.

External crown surface area is the upper surface of a solid object of the size and shape of the tree crown, excluding non-foliar portions, such as the spreading area of limbs under the canopy. The number of acorns from each of 18 trees with total acorn counts was divided by the external surface area of the crown to give acorns/m^2 of external crown area. Calculations were made for the top half of the green crown, the bottom half of the green crown, and the total green crown. Acorns/m^2 for all 18 trees were averaged by top half, bottom half, and the entire canopy for each acorn class to quantify the acorn abundance classes.

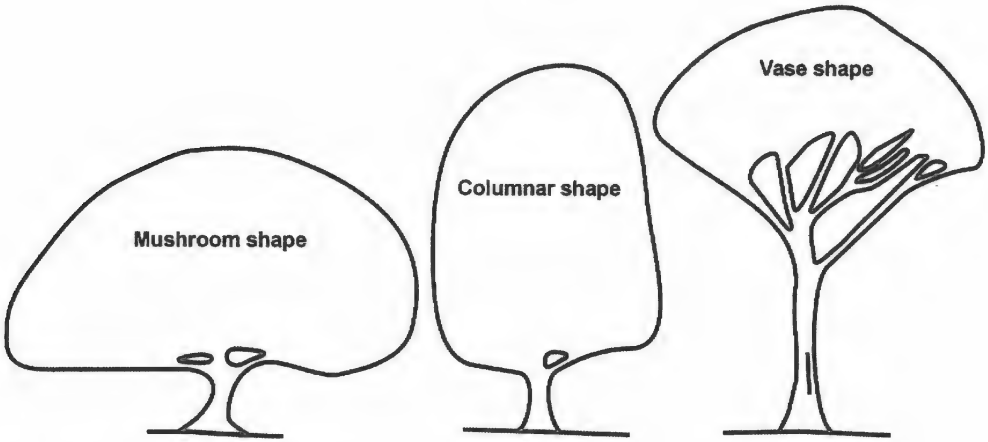

Figure 2. Canopy shapes assigned to oak trees in acorn survey. No relationship between shape and height is implied.

Health

We examined the broad effects of tree health on acorn productivity with a simple class system. Healthy trees had all bark and major limbs present and alive, no visible rot, and full crown of healthy leaves. Moderately healthy trees had some missing bark, broken major limbs, or visible rot, but otherwise appeared healthy. Unhealthy trees had much visible rot, sparse foliage, or major branches broken or dead.

Age

We extracted increment cores at 1.3 m above ground from 73 trees and counted rings to assess the effect of tree age on acorn productivity. Of these, 22 hit the pith, 36 were judged to be within 10 rings and an estimate was added to the ring count, and 15 missed the pith by more than 10 rings. An age-diameter relationship was calculated from complete cores for use in estimating total age at 1.3 m from cores judged to have missed the pith by more than 10 rings. A straight line was regressed through age/diameter data from 16 Puget Sound area trees < 50 yr old (age=16.23+1.14 dbh (cm.); r^2=0.56). This relationship was used to estimate numbers of missing rings to pith from the inside of incomplete increment cores. Age at 1.3 m was used rather than total age because it is easier to obtain and the variation in the years between age at 0 m and age at 1.3 m is too great to allow extrapolation. The relationship of age to acorn abundance was examined by determining the percent of the sample in each abundance class by 20-yr age groups.

Underburning

The effect of prescribed burning on acorn productivity was examined by displaying the percent of trees in each acorn class by years since the last prescribed underburn. Underburns are fires that do not ignite the canopy of the overstory and generally have flame lengths < 3 m. Underburning is prescribed for fuel reduction, to modify understory composition or to arrest succession toward conifer dominance. In most cases the severity of the underburn was not known, but fire-damaged boles and lower limbs were observed on many trees. Years since the last underburn was known for 55 trees. Most of these trees were on Fort Lewis, but eight were from Oak Patch Natural Area Preserve on the Kitsap Peninsula, Washington. Both locations are in the south Puget Sound area on similar Spanaway or Everett soils. An additional 119 trees on similar soils in the same general area, including trees from Oak Patch and Fort Lewis, were judged not to have been underburned in 20 yr or more and were compared with those with known burning history.

Statistical Analysis

We used ANOVA and logistic regression to examine relationships in the data. Since acorn production class is not normally distributed, standard statistical procedures were not appropriate in all instances, so that both non-parametric and parametric techniques were used. The level for statistical significance was set at P=0.05.

We used Kruskal-Wallis nonparametric ANOVA (Zar 1999) to test for differences in acorn code distribution between categories of the independent moisture variables: precipitation, AWC, and moisture index. Data for the moisture variables were assigned to groups by dividing the range into thirds, so that there was a low, medium, and high group for each independent variable (Table 3). A fourth group was added to cover trees that received supplemental irrigation. The null hypothesis of no difference in acorn code distribution

TABLE 3. Characteristics of moisture analysis groups for Kruskal-Wallis ANOVA. *P* is the probability that there is a difference in distribution of acorn codes between the moisture classes.

	Available Water Capacity			Precipitation			Moisture Index		
Group	Mean	n	Acorn code rank mean	Mean (cm)	n	Acorn code rank mean	Mean index	n	Acorn code rank mean
Low	4.3	13	75	64	10	122	5.8	15	74
Medium	10.0	238	140	111	209	136	12.2	241	141
High	22.2	16	143	170	48	143	26.1	11	127
Irrigation	4.0	10	190	105	10	190	2.5	10	189
P	-	-	0.0022	-	-	0.1244	-	-	0.0007

among the four groups was tested for each independent variable. When the ANOVA indicated significance, we compared the groups with a Dunn test (Zar 1999).

We also used Kruskal-Wallis nonparametric ANOVA to analyze distribution differences in acorn abundance code between health class groups. When the ANOVA indicated significance, we compared health groups with a Dunn test.

We used parametric ANOVA to characterize the basal area and crown contact environments around sample trees in different acorn production classes. We determined which groups were different with Duncan's Multiple Range Test when the ANOVA indicated significant results.

To evaluate the effects of competition on acorn production of the sample trees, we used logistic regression with acorn code as the dependent variable (Allison 1999, SAS Institute Inc. 2000). Basal area of the surrounding stand, percent crown contact of the sample tree with surrounding trees, and crown shape were the independent variables. Logistic regression estimates the probability of a certain event occurring by calculating changes in the log probability of the dependent variable. For this analysis we reduced the acorn production data to two classes: nonproducing and producing (i.e. light and medium producing were combined into one class). There were 96 trees with basal area data, 124 trees with crown shape data, and 245 trees with percent crown contact data. Figure 3 was produced by plotting logistic regression output for the probability of acorn production at each 10% interval of crown contact.

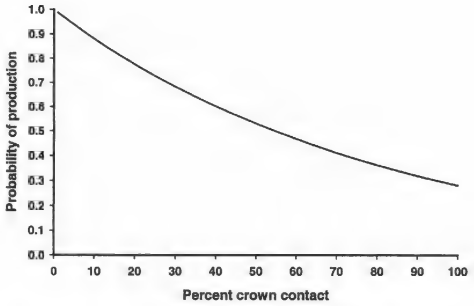

Figure 3. The probability of acorn production as a function of the percent crown contact.

Results

Site Characteristics

There were 68 sample trees growing on slopes > 3°; 45 were on south or west aspects, and 24 on north or east aspects. Due to wide variation in elevation and soil type of tree sites with slopes > 3°, it would not be meaningful to test for differences due to aspect.

Moisture

A wide variety of moisture conditions was represented on the survey sites (Table 4). In 1999, productivity was highest on well-drained irrigated soils and lowest on extremely dry or wet soils in our sample. There was a significant difference in acorn code distribution between soils with low, medium, or high available water capacity and irrigated soils (P=0.002) (Table 3). The low AWC group, which had the lowest overall productivity distribution had significantly lower acorn production than the irrigated group, which had the highest overall productivity distribution. Precipitation alone had no significant effect on acorn productivity, but when precipitation was combined with AWC into a moisture index there was a significant difference in acorn code distribution between low, medium, and high moisture index and irrigated groups (P=0.0001) (Table 3). All groups were significantly different from each other except the moderate and moist index groups. The lowest productivity distribution was in the low index group and the highest in the irrigated index group. Another group of five trees growing in a slough sedge (*Carex obnupta*) wetland was not included in this analysis but produced few acorns in 1999.

Tree Characteristics

Tree dimensions by geographic area ranged from 5-22 m tall, 4-19 m wide, and 20-108 cm diameter at 1.3m. Overall, there were 47% nonproducing trees, 34% light-producing trees, and 19% medium-producing trees in our sample. There were no heavily-producing trees in the 1999 sample. Most of the sample trees were dominant, codominant, or open grown but some were intermediate or suppressed. In 18 trees with complete counts, acorn density was greater in the top half of the canopy than the bottom half, and greater in medium-producing trees than non- or light-producing trees (Table 5). Mean tree surface area in-

TABLE 4. Percent of sample in each acorn class by soil series and soil moisture characteristics. Soil series are sorted by percent of nonproducing trees.

Soil Series (with treatments or amendments)	AWC[1]	Annual precipitation[2] (cm)	Moisture index[3]	Percent of trees in each acorn class			
				None	Light	Medium	n
Prather silty clay loam (fertilized)	21	119	26	0	0	100	2
Panther silty clay loam	24	114	27	0	0	100	1
Townsend sandy loam (fertilized, irrigated)	4	64	3	0	40	60	5
Nisqually loamy sand	12	117	14	14	43	43	7
Sequim very gravelly sandy loam (fertilized, irrigated)	4	48	2	20	80	0	5
Oakland silt loam	13	99	13	20	80	0	5
Carstairs very gravelly loam	8	168	14	22	44	33	9
Wamic loam	20	58	12	40	0	60	5
Pengra silt loam	20	114	23	40	20	40	5
Everett gravelly sandy loam and gravelly loam	9	142	13	41	18	41	17
Spanaway gravelly sandy loam	10	117	12	46	38	16	173
Atring gravelly loam	10	114	12	50	50	0	2
Spanaway stony sandy loam	10	130	13	67	33	0	3
Fitch gravelly sandy loam	10	104	10	70	30	0	10
Ritner gravelly silty clay loam	11	104	11	75	25	0	4
Wetlands	-	130	-	80	20	0	5
Nonpareil-Oakland complex	7	94	7	80	20	0	5
Fricaba extremely gravelly sandy loam	3	318	11	100	0	0	3
Waketickeh extremely gravelly sandy loam	1	318	4	100	0	0	3
San Juan gravelly sandy loam	9	69	6	100	0	0	5
Philomath-Edenbower complex	7	104	7	100	0	0	1
Veneta loam	27	94	25	100	0	0	5

[1]AWC = available water capacity in the top 150 cm of soils (USDA, NRCS 1994).

[2]Average annual precipitation from PRISM data (USDA NRCS and OSU 1999).

[3]Moisture index = precipitation x AWC/100

TABLE 5. Mean number of acorns per square meter and external crown surface area (±SE) by acorn class for the subsample of trees that had complete acorn counts. All trees were from the South Puget Sound or Fort Lewis areas.

Acorn class	n	Portion of crown			External crown surface area (m^2)[2]
		Top	Bottom	Total[1]	
None	9	0.03	0.03	0.03	180
Light	5	0.30	0.08	0.19	233
Medium	4	2.64	0.72	1.60	368

[1]Standard errors for total number of acorns were 0.03 for nonproducers, 0.05 for light producers, and 0.6 for medium producers.

[2]Standard errors for crown surface area were 100, 46, 57.

creased with acorn class. Sample trees classed as medium producing not only produced a greater density of acorns but also had more crown surface area than the non or light producing trees.

Health

Most trees were rated as moderately healthy or healthy, but 16% were unhealthy. Differences in acorn class distribution between the three health classes were significant (P=0.003). The unhealthy tree group had a significantly lower acorn class distribution than the moderately healthy or healthy trees. Trees rated as healthy or moderately healthy were not significantly different.

Shape

Tree shapes were important indicators of productivity because they reflect the competitive environment around the tree. Overall, the sample had more vase-shaped trees (40%), than mushroom-shaped trees (35%), or columnar-shaped trees (25%), although proportions varied by site. Vase shaped trees comprised the highest percent of nonproducing trees and the lowest percent of

TABLE 6. Percent of sample trees by shape class and acorn class.

Acorn class	Tree shape		
	Vase	Columnar	Mushroom
Nonproducing	66	49	28
Light	30	41	41
Medium	5	11	31
Sample size	61	38	54

medium-producing trees (Table 6). The highest percent of producing trees were mushroom-shaped (72%). The effect of crown shape on probability of production in a binomial logistic regression was significant (P=0.004). Vase shaped trees were significantly greater than mushroom-shaped trees (P=0.0001).

Crown Contact

Percent crown contact ranged from 0 to 100% but averaged from 25% to 65% in different areas (Table 2). Percent crown contact and tree shape were related. Crown contact was 56% for vase, 33% for columnar, and 33% for mushroom shaped trees in our sample. Percent crown contact for vase-shaped trees was significantly greater than columnar- or mushroom-shaped trees (P=0.0001), which were not different from each other.

The effect of crown contact on probability of production in a binomial logistic regression was significant (P=0.005). As percent crown contact increased the probability of acorn production decreased in our sample (Figure 3). For example, a 20% increase in crown contact resulted in changing the odds of production by 0.73, so that if crown contact increases by 20%, the probability of acorn production decreases by 27%.

Basal Area

Mean stand basal area around the sample trees ranged from 4-20 m^2/ha by geographic area (Table 2). Mean basal area surrounding the sample trees was 7 m^2/ha in trees with medium production, 12 m^2/ha in trees with light production and 16 m^2/ha in trees with no acorn production (Table 7). The effect of basal area on the probability of acorn production was significant (P=0.02). A 10 m^2/ha increase in basal area would be expected to change the odds of production by 0.64 (36% decrease in the likelihood that the tree would produce).

TABLE 7. Basal area (m^2/ha) and number of sample trees by acorn class.

Acorn class	Mean	Standard error	n
Nonproducing	16	2.2	110
Light	12	1.6	86
Medium	7	1.6	49

Age

Ages clustered around 100 yr, but individual trees varied from 11 to > 300 yr at 1.3 m. No acorns were found in trees younger than 20 yr even though they were open grown (Figure 4). Between age 20 and 80 yr, the percent of nonproducing trees decreased and medium producing trees increased. In the 60-79-yr group, 41% of the trees were nonproducing, 40% light producing, and 19% medium producing. There was no apparent trend in productivity after 80 yr. Trees older than 180 yr were mostly in the light- and nonproducing classes, and the oldest and largest tree (> 300 yr) in our sample produced no acorns despite its healthy appearance.

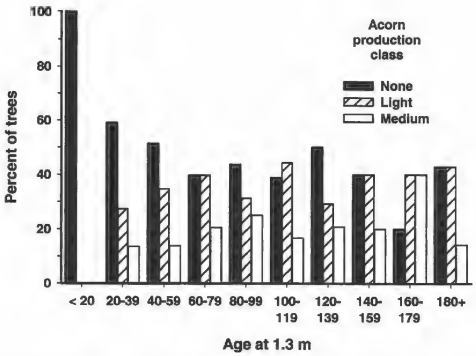

Figure 4. Percent of sample trees by acorn abundance class and age at 1.3 m.

Fire

There was an apparent relationship between acorn productivity and underburning history (Figure 5). Among sample trees underburned one year prior to survey, 71% were nonproducing. This compares to only 48% nonproducing trees in the unburned sample. Two to four years post-burning, sample trees averaged nearly the same percentage of nonproducing trees and medium-producing trees as unburned trees. Trees underburned

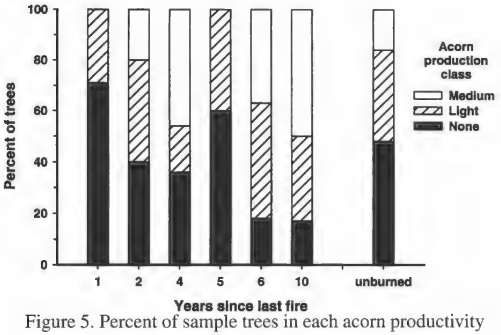

Figure 5. Percent of sample trees in each acorn productivity class by years since last fire.

6-10 yr ago produced much better acorn crops on average than non-burned trees. They had only 18% nonproducing trees compared to 48% in the non-burned group. They also had 41% medium-producing trees compared to 16% in the non-burned group.

Discussion

In general acorn production in our sample was influenced by competition (measured by basal area, tree shape, and crown contact), moisture (indicated by precipitation, AWC, and moisture index), age, and fire history. Productivity tended to be highest on well watered, well drained sites on trees at least 60-80 yr old that were growing under little competition from neighbors. The effect of fire history was more complex. Our data at least suggest that prescribed underburning may reduce acorn production in the year immediately following burning, but may also contribute to higher production 6-10 yr after underburning.

Annual variations in acorn crop size complicate the interpretation of acorn production. There is little published information on acorn crop sizes in Oregon white oak with which to compare these data. We believe that the 1999 acorn crop was moderate. In contrast the 1998 acorn crop was small at Fort Lewis (Andrew B. Carey, Pacific Northwest Research Station, Olympia, Washington, personal communication).

Large acorn crops occur every few years in Oregon white oak (Harlow and Harrar 1958). Coblentz (1980) followed acorn production on Oregon white oaks in the Willamette Valley for 3 yr and found one good crop, one moderate crop, and one crop failure. Good seed crops for blue oak (*Quercus douglasii*) were observed every 2-3 yr, with larger crops every 5-8 yr (Olson 1974) or in 4 of 7 yr with one bumper crop (Carmen et al. 1987). Valley oak (*Quercus lobata*), another white oak species, had a similar pattern, with small crops in 5 of 7 yr and one bumper crop (Carmen et al. 1987). If acorn production varies widely in different years it remains to be seen if the patterns of acorn production found in this study change or simply shift in magnitude.

Oregon white oak has wide ecological amplitude, growing on sites that are seasonally flooded to excessively drained with low water-holding capacity. Presumably all sites are capable of acorn production in some years. In 1999, however, little production was observed in our sample where the moisture index was low or on poorly drained soils (Table 4). In addition, productivity was higher than would otherwise have been expected on droughty soils receiving supplemental irrigation suggesting that water was frequently limiting in 1999. Productivity was highest on moist, well-drained soils and generally declined as water availability declined or on poorly drained sites.

The sites that did not fit the pattern of declining acorn productivity with declining water availability are the Pengra silt loam, Veneta loam, and wetlands (Table 4). Based on soil texture and location we expect these soils to have abundant soil moisture through the growing season. Trees growing in wetlands may have a shallower distribution of roots than trees on better-drained sites, making it difficult to assess water availability during the time of acorn development using an index based on standard soil depth. Pengra silt loam is somewhat poorly drained with a high water table from November to May so that trees on this soil may also have a shallow root system. The Veneta loam is moderately well drained with a high AWC and moisture index, thus would be expected to have a deep root system and to produce well. Trees on this soil may produce well in other years.

In our sample there was an indication that tree age affects productivity with production starting around 20 yr increasing to around 60-80 yr, then leveling off (Figure 4). The oldest tree in the sample (> 300 yr) produced no acorns in 1999, but there was no clear decline in productivity associated with increasing age in the sample. A similar age related pattern was found in California black oak (*Quercus kelloggii*), which begins acorn production at 30 yr, but does not produce large quantities

on a regular basis until 80-100 yr. California black oak acorn production increases until at least 200 yr of age (McDonald 1990). We suspect that site quality characteristics and competitive conditions influence the onset of production. Our age data are not complete enough to show a difference in onset of acorn production between forest and open-grown trees, but the youngest producing trees in our sample were open grown.

Competition with other trees was an important factor in acorn production in our sample. As competition increased, crown contact and basal area increased and tree shape changed. Oregon white oak is not shade tolerant and will lose lower limbs under lateral shade, resulting in the vase shape typical of trees growing in dense stands (Stein 1990). Crown shape, although only measured on a subset of trees, was an easy variable to code and a good predictor of productivity (Table 6). High irradiances are associated with increased flowering in many plants (Halevy 1983, Krugman et al. 1974). It makes sense that in a species that produces acorns mostly on branch tips in full sun, a measure like crown shape, which provides an indication of light availability to the crown, would be effective. Our data set on crown shape was entirely composed of trees from stands that had not been thinned. Since acorns are an important food source for wildlife, maintaining acorn production is a management concern. The relationship of open-grown crown shapes, low crown contact, and low basal area to higher productivity suggests thinning is an option for increasing acorn production in forest stands, but we do not know how well Oregon white oak responds to thinning. If Oregon white oak responds to thinning, crown shape would be a simple criteria for selecting trees for release treatments, and for gauging recovery.

Basal area and crown contact were also significant predictors of acorn productivity in our sample (Table7, Figure 3), but were somewhat less effective than crown shape (Table 6). We assume shape was important because it serves as an integrator of the competitive environment around the tree for an extended time period. In managed stands we suspect that both a shape variable (indicating past environment) and a measure of current competition (such as crown contact or basal area) would be important. In addition, it appears that young trees with good apical dominance and older trees receiving side light can both have columnar shapes. Adding age, or an age-surrogate such as height, may be useful in separating columnar trees into groups with less variation in acorn production.

In our sample open-grown trees are better acorn producers than crowded trees (Table 6, Figure 3), which is what Coblentz (1980) reported. Our measures of acorn productivity (the codes or the counts on a subsample of trees) were tree based. We do not know what level of stand density would result in the best productivity per unit area. A forest of vase shaped oak trees may have higher acorn production per unit of land than a savanna of mushroom shaped trees because every area in the forest is producing acorns. The relationships between tree- and stand-based measures of acorn productivity will need to be evaluated to provide managers with better tools to make decisions.

Underburning is a useful management tool for reducing shrub and tree competition around Oregon white oak, but it may affect acorn productivity. This is an important consideration when managing acorn-consuming species such as the threatened (in Washington) western gray squirrel. The data suggest that underburning at the intensities sampled for this study causes an initial loss of acorn productivity relative to unburned trees in the year after the burn (Figure 5). The mechanisms by which burning can impact acorn productivity have not been studied, but probably vary depending on site, tree characteristics, and intensity and duration of the fire. Following a recovery period of one to several years, productivity on burned areas may be enhanced relative to unburned trees. This relationship implies a reproductive benefit to trees following underburning and recovery, but the duration of the benefit is unknown. Most of the underburned trees in this study had a shrub understory component at the time of burning, which made fires more intense. Low intensity grass fires probably cause less tree damage and may not result in an initial loss of acorn production. This would have important implications for managers of oak stands using prescribed fire.

Acknowledgements

We wish to thank Fort Lewis, especially Gary McCausland and the Fort Lewis Forestry Department, for providing financial and logistical support to this project. We also thank the landowners

and managers who granted access to private or restricted public lands, and the Washington Department of Natural Resources and the Oregon Department of Fish and Wildlife for permitting employees to participate in the survey. Special thanks go to the volunteers who helped us to greatly expand and extend our sample of oak trees.

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Received 5 April 2001
Accepted for publication 18 March 2002

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Gordon D. Nigh,[1] Research Branch, British Columbia Ministry of Forests, P.O. Box 9519, Stn. Prov. Govt., Victoria, British Columbia, Canada V8W 9C2

Pavel V. Krestov, Institute of Biology and Pedology, Russian Academy of Sciences, Far Eastern Branch, Vladivostok, Russia V690022

and

Karel Klinka, University of British Columbia, Department of Forest Sciences, 3041 - 2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4

Trembling Aspen Height-Age Models for British Columbia

Abstract

Trembling aspen, a common hardwood species in the interior of British Columbia, is becoming an increasingly important timber crop species, especially in the northeast corner of the province. Better growth and yield information for aspen is required to manage this species properly. We provide height-age models for estimating site height and site index. One-hundred and thirty-five stem analysis plots were established in six biogeoclimatic zones. Three trees in the 0.04 ha plots were selected and stem analyzed, and ecological data were collected at each plot. The stem analysis data were split into a model calibration and test data set. Two models were fit to the calibration data: a base model and an extended model that is calibrated for the six biogeoclimatic zones. Both models adequately estimate the height of trembling aspen in British Columbia. The base model was compared to two models for aspen in Alberta, which showed that there were no large differences in the height growth of aspen, except on lower productivity sites.

Introduction

Trembling aspen (*Populus tremuloides*) is the most widespread hardwood species throughout North America (Perala 1990). Its range extends across Canada to the northern tree line. In the United States, it is found mainly in the western mountains, and around the Great Lakes east to the Atlantic Ocean. As might be expected for a species with such a broad geographic range, it grows in a wide variety of climatic and soil conditions.

In British Columbia, aspen occurs throughout most of the interior of the province and, to a minor extent, on the southeast coast of Vancouver Island and along the mouths of the Fraser and Skeena rivers (Klinka et al. 2000). Aspen is most frequent in the Boreal White and Black Spruce (BWBS), Sub-Boreal Spruce (SBS), and Interior Douglas-fir (IDF) biogeoclimatic zones, and less frequent in the Montane Spruce (MS) and Interior Cedar-Hemlock (ICH) zones (Klinka et al. 2000). A description of the biogeoclimatic zones can be found in Meidinger and Pojar (1991).

Aspen often grows in pure, even-aged stands. It associates frequently with white spruce (*Picea glauca*), mainly in the BWBS and SBS zones, and is frequently found with lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) (Klinka et al. 2000). It is a shade intolerant species that typically regenerates by root suckering, especially after fire or clearcutting. Aspen has become an important timber species in British Columbia. It is used for lumber, pulp, and oriented strand-board, and also provides valuable non-commercial resources such as wildlife habitat, forest biodiversity, and livestock forage areas (Peterson and Peterson 1995, Klinka et al. 2000).

As the importance of trembling aspen increases, better growth and yield information will be required for this species. The only growth and yield model available in British Columbia that is calibrated for aspen is the Variable Density Yield Prediction (VDYP) system (Ministry of Forests 1997). The Mixedwood Growth Model (MGM) (Titus 1998) is in the process of being adapted for British Columbia forests. Both MGM and VDYP use site index models developed for aspen in Alberta (Alberta Forest Service 1985). Evidence suggests that these models may be biased when estimating aspen height growth in British Columbia (Chen

[1] Author to whom correspondence should be sent. E-mail: Gordon.Nigh@gems2.gov.bc.ca

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et al. 1998). Therefore, recommendations for developing MGM include new site index models for British Columbia (Harper 2000). The purpose of this project is to develop site index models for trembling aspen with data collected in the biogeoclimatic zones in which aspen is mainly found. In this project, we develop models that provide reliable estimates of height and site index for growth and yield, and for other management purposes.

Methods

Height-Age Data

The data for this project were collected as part of a study to develop the classification of aspen ecosystems in British Columbia and aspen productivity (Krestov et al. 2000). Additional information about the data can be found in Krestov et al. (2000). One-hundred and eighty-six plots were established in the BWBS (88 plots), SBS (25), Sub-Boreal Pine-Spruce (SBPS) (7), IDF (23), MS (19), and ICH (24) biogeoclimatic zones. Of these plots, 135 were available for developing site index models. Trees from the other 51 plots were either too young (they must be at least 50 yr old at breast height so that the site index is known) or were suppressed or damaged (often decayed) in some way that precluded their use. Trees with damage or suppression would bias the site index. The plots were located to cover a wide range in climate, topography, soil moisture, and nutrient conditions.

The 20 m × 20 m study plots were located in naturally established, unmanaged, fully stocked (the cover of the tree layer was >75%), even-aged stands. Each stand had a uniform canopy of trembling aspen, understory vegetation, and site. Site, vegetation, and soil were described according to Luttmerding et al. (1990). Three largest diameter dominant aspen trees were selected from each plot for stem analysis. At the time of selection, these trees had no visible signs of damage or suppression so that their height growth adequately reflected the productivity of the site. The trees were cut down and sections were taken at 0.3 m, 0.8 m, 1.3 m, and at 1-m intervals above 1.3 m. The rings on each section were counted in two directions under magnification. Suppressed growth was checked at this time and suppressed trees were deleted from further analyses.

The section height-ring count data were converted into height-breast height age data by standard methods (Carmean 1972, Dyer and Bailey 1987, Newberry 1991). Individual tree height trajectories were plotted to detect damage, errors in ring counts, and as a final check for suppression. Errors in ring counts were corrected and damaged/suppressed trees were deleted. If more than one tree in a plot was rejected, then the whole plot was excluded from the analysis. The individual tree height-breast height age data were averaged by age within plot to get site height-breast height age data. The site height at breast height age 50 is site index by definition.

Height-Age Models

The data were split into a model calibration and a model testing data set by first sorting the plots by biogeoclimatic zone. Every second plot was put into a calibration data set and the remaining plots were put into a test data set, which created balanced data sets with respect to zone. We wanted to have an approximately equal number of plots from each zone in the calibration and test data sets because we tested for differences in growth pattern between zones. The calibration and test data sets consisted of heights at 5 yr intervals starting at age 5, except the test data set excluded the height at breast height age 50 because the model is conditioned to be exact at that age.

Two models were developed: a base model and an extended model to test for differences in height growth patterns across biogeoclimatic zones.

Base Model

The functional form for the base height-age model is the logistic function (1).

(1)

$$HT = 1.3+(SI-1.3)\times\frac{1+e^{a_0+a_1\times\ln(49.5)+a_2\times\ln(SI-1.3)}}{1+e^{a_0+a_1\times\ln(BHA-0.5)+a_2\times\ln(SI-1.3)}}$$

where HT is site height (m), SI is site index (m), BHA is breast height age (yr), e is the base for natural logarithms, ln is the natural logarithm operator, and a_0, a_1, and a_2 are model parameters. This function has been used successfully in other height growth modelling projects, and it seems to work quite well across a broad range of species (Thrower and Goudie 1992; Nigh 1997; Chen and Klinka 2000).

Equation (1) with an AR(1) error term was fitted to the calibration data using weighted nonlinear regression. The AR(1) model is a first-order autoregressive model that accounts for serial correlation that usually exists with stem analysis data. The AR(1) model is given in (2).

$$\varepsilon_{i,BHA} = \phi \times \varepsilon_{i,BHA-10} + \omega_{i,BHA} \quad (2)$$

where $\varepsilon_{i,BHA}$ is the error term for plot i at BHA, ϕ is the autocorrelation coefficient ($-1 < \phi < 1$), and the $\omega_{i,BHA}$'s are normally distributed independent random errors with mean zero and constant variance. The weighting was done to stabilize the variance. Both sides of the model were divided by a weight (wt) as given in (3).

$$wt = \begin{cases} BHA^{-0.25} & \text{if BHA <25,} \\ abs(50-BHA)^{-0.25} & \text{otherwise} \end{cases} \quad (3)$$

where abs is the absolute value operator.

Extended Model

The extended model was created by introducing indicator variables into the base model that allow the value of the parameters a_0, a_1, and a_2 to vary across zones, as shown in (4).

$$a_0 = a_{00} + a_{01} \times ICH + a_{02} \times IDF + a_{03} \times MS + a_{04} \times SBPS + a_{05} \times SBS \quad (4)$$

$$a_1 = a_{10} + a_{11} \times ICH + a_{12} \times IDF + a_{13} \times MS + a_{14} \times SBPS + a_{15} \times SBS$$

$$a_2 = a_{20} + a_{21} \times ICH + a_{22} \times IDF + a_{23} \times MS + a_{24} \times SBPS + a_{25} \times SBS$$

where ICH is 1 if the plot is in the ICH zone, 0 otherwise, IDF is 1 if the plot is in the IDF zone, 0 otherwise, MS is 1 if the plot is in the MS zone, 0 otherwise, SBPS is 1 if the plot is in the SBPS zone, 0 otherwise, SBS is 1 if the plot is in the SBS zone, 0 otherwise. Parameters were deleted if they were not significantly different from 0. Terms were combined if their parameter estimates were similar, that is, if the confidence interval of one parameter enveloped the estimate of the other parameter, and vice versa. Although this method is not optimal, it is easy to implement and will lead to zones being incorrectly deemed as being different (Schenker and Gentleman 2001), which complicates the model but does not cause bias. As before, an AR(1) error term was added and weighted regression was used to estimate the parameters, but using (5) as a weighting function.

$$wt = \begin{cases} BHA^{-0.30} & \text{if BHA <25,} \\ abs(50-BHA)^{-0.30} & \text{otherwise} \end{cases} \quad (5)$$

It was critical to meet the regression assumptions for both the base and extended models. A violation of one or more of the Gauss-Markov conditions (the residuals are uncorrelated, have a mean of zero, and a constant variance) generally does not bias the parameter estimates, but it will bias the variances of the parameter estimates (Sen and Srivastava 1990). Biased variances will lead to biased t-tests and perhaps wrong conclusions when testing for differences between zones, although moderate heteroscedasticity does not seriously impact the results of tests on parameter estimates (Mason et al. 1989). Non-normality of the residuals may also lead to wrong conclusions because the t-test is based on normally distributed populations. However, the t-test is robust against slight deviations from normality (Mason et al. 1989). The regression assumptions were checked with the following tests:

1. expected value of the residuals is zero: a t-test;
2. normality: W test (Shapiro and Wilk 1965);
3. constant variance: plots of residuals against breast height age and site index, and the F_{kk} test (Endrenyi and Kwong 1981);
4. correlated residuals: plots of residuals against breast height age, by plot, and correlations between the residuals and their lag, by plot.

The weighting functions (3) and (5) affected all of the above tests. Much effort was expended in meeting all the regression assumptions.

The base model and the extended model were tested by using the models (and the breast height age and site index in the test data) to estimate the heights in the test data set. The errors in the height estimates were calculated by subtracting the estimated height from the actual height. The mean error and its standard error were calculated for all the observations, and for the observations for each age and within biogeoclimatic zone. We conducted t-tests on the mean errors to detect statistical bias, that is, to check whether the mean error was significantly different from zero.

Results

The distribution of the calibration and test data sets is even, with approximately equal means, minimums, and maximums for both data sets (Table 1). The balance between the two data sets means that the calibration and testing procedures equally weight the range of site indices, heights, and ages. This balance was not found across biogeoclimatic zones (Table 2). The MS and ICH zones have the highest mean and maximum site indices of all the zones (Table 2). Note, however, that the sampling was not random so that statistically-based conclusions cannot be drawn.

TABLE 1. Summary statistics for the trembling aspen stem analysis data (by data set).

	Number of plots	Minimum	Mean	Maximum
Calibration data set				
Height (m)	68	7.27	20.42	37.50
Breast height age (yr)	68	50	78	177
Site index (m)	68	6.81	16.72	29.56
Test data set				
Height (m)	67	5.74	20.61	36.00
Age (yr)	67	50	76	159
Site index (m)	67	5.60	16.61	28.73
Both data sets				
Height (m)	135	5.74	20.51	37.50
Age (yr)	135	50	77	177
Site index (m)	135	5.60	16.66	29.56

This study presents two new models for estimating the height of trembling aspen site trees in British Columbia: a base model and an extended model. The base model is a general model that could be used anywhere in British Columbia, or when the biogeoclimatic zone is unknown.

$$HT = 1.3+(SI-1.3)\times\frac{1+e^{7.423-1.150\times\ln(49.5)-0.9614\times\ln(SI-1.3)}}{1+e^{7.423-1.150\times\ln(BHA-0.5)-0.9892\times\ln(SI-1.3)}}$$

The parameter estimates and their standard errors, the mean error and *P*-value of the associated t-test for bias, the W statistic and *P*-value for normality, and the F_{kk} test and *P*-value for constant variance are used to evaluate the model (Table 3). These statistics show that the model is unbiased and has normally distributed, homoscedastic residuals. In addition, only five plots had statistically significant correlation in the lagged residuals. Therefore, we conclude that the regression assumptions were adequately met. The residuals plotted against breast height age and site index demonstrate the constant variance and, to some extent, the low correlation between residuals (Figure 1). Although the variance of the residuals appears to be declining with age, a small number of data points at older ages can give the appearance of heteroscedasticity (Carroll and Ruppert 1988).

TABLE 2. Summary statistics for the trembling aspen stem analysis data by biogeoclimatic zone.

	Number of plots	Minimum	Mean	Maximum
Boreal White and Black Spruce zone				
Height (m)	56	5.74	16.65	26.25
Breast height age (yr)	56	50	79	177
Site index (m)	56	5.60	13.69	25.24
Interior Cedar-Hemlock zone				
Height (m)	16	15.33	25.73	37.50
Age (yr)	16	55	75	99
Site index (m)	16	12.46	21.15	29.56
Interior Douglas-fir zone				
Height (m)	18	9.25	21.30	29.37
Age (yr)	18	54	74	119
Site index (m)	18	8.71	17.18	23.99
Montane Spruce zone				
Height (m)	18	12.65	25.26	31.20
Age (yr)	18	53	62	74
Site index (m)	18	12.22	22.19	29.27
Sub-Boreal Pine-Spruce zone				
Height (m)	7	11.33	17.63	24.57
Age (yr)	7	50	72	114
Site index (m)	7	9.24	15.07	22.33
Sub-Boreal Spruce zone				
Height (m)	20	16.69	23.20	30.02
Age (yr)	20	53	92	153
Site index (m)	20	10.35	16.51	23.10

TABLE 3. Results of the analysis of the base model.

Statistic	Estimate	Standard error (or *P*-value)	95% confidence interval Lower	Upper
Parameter a_0	7.423	0.2758	6.881	7.965
Parameter a_1	-1.150	0.02324	-1.196	-1.104
Parameter a_2	-0.9614	0.09335	-1.145	-0.7780
Parameter ϕ	0.9892	0.02151	0.9470	1.031
Mean error	0.009847	(0.8353)		
W	0.9805	(0.0769)		
F_{kk}	1.143	(0.2206)		

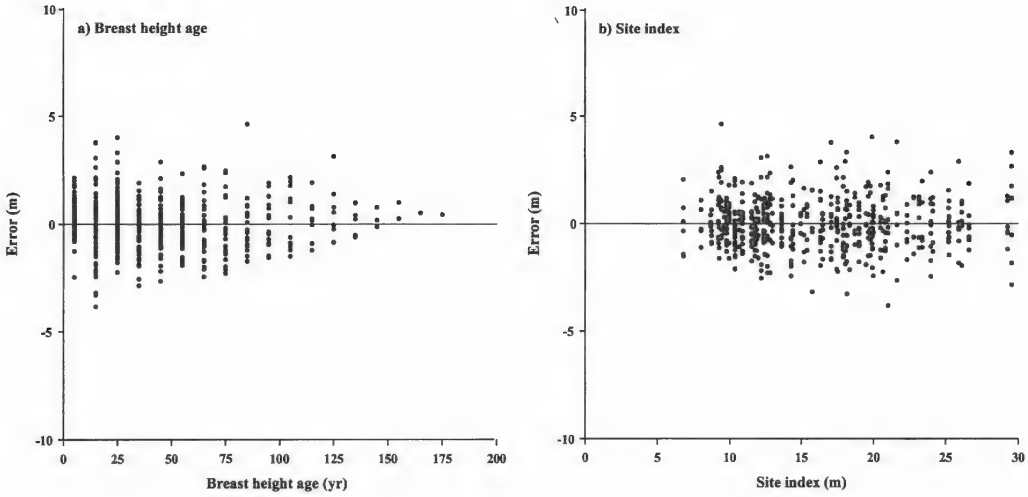


Figure 1. Residuals from the base model (1) plotted against breast height age (part a) and site index (part b). Note that the errors are weighted.

The extended model is calibrated specifically to six major biogeoclimatic zones where trembling aspen is the major species.

$$HT = 1.3+(SI-1.3)\times\frac{1+e^{a_0+a_1\times\ln(49.5)+a_2\times\ln(SI-1.3)}}{1+e^{a_0+a_1\times\ln(BHA-0.5)+a_2\times\ln(SI-1.3)}}$$

where a_0 = 7.314 (for the BWBS, IDF, MS, and SBPS zones) or 8.363 (for the ICH and SBS zones), a_1 = -1.074 (for the BWBS, IDF, and SBS zones) or -1.446 (for the ICH zone) or -1.243 (for the MS and SBPS zones), and a_2 = -1.011 (for the BWBS, ICH, and IDF zones) or -0.9080 (for the MS and SBPS zones) or -1.267 (for the SBS zone). The results of the regression analysis of the extended model are in Table 4. Not all parameters in parameter set (4) are included in the extended model. The parameters in the final extended model are the result of testing many different combinations of parameters to determine which could be grouped together. The statistical tests (Table 4) show that the model is unbiased and the residuals are normally distributed and homoscedastic. Only five plots had lagged residuals that were correlated. Graphs of the residuals from the extended model plotted against breast height age and site index support our conclusion that the regression assumptions have been met (Figure 2).

The model testing shows that the both models are generally good at estimating height. Although some biogeoclimatic zones show statistical bias, it is probably insignificant in practice (Table 5). The mean error in height across age is also small (Figure 3), except at extremely old ages, which is likely a result of only having a few plots at older ages.

We graphically compared the base model to the trembling aspen model currently used in British Columbia (Alberta Forest Service 1985) and the

TABLE 4. Results of the analysis of the extended model.

Statistic	Estimate	Standard error (or *P*-value)	95% confidence interval Lower	Upper
Parameter a_{00}	7.314	0.2878	6.749	7.879
Parameter a_{01}	1.049	0.1806	0.6944	1.404
Parameter a_{10}	-1.074	0.02767	-1.128	-1.020
Parameter a_{11}	-0.3723	0.06981	-0.5095	-0.2352
Parameter a_{12}	-0.1694	0.05408	-0.2757	-0.06319
Parameter a_{20}	-1.011	0.1031	-1.213	-0.8083
Parameter a_{21}	0.1030	0.04315	0.01821	0.1878
Parameter a_{22}	-0.2562	0.07059	-0.3948	-0.1175
Parameter ϕ	0.9942	0.02065	0.9536	1.035
Mean error	-0.00476	(0.9267)		
W	0.9832	(0.2683)		
F_{kk}	1.059	(0.3714)		

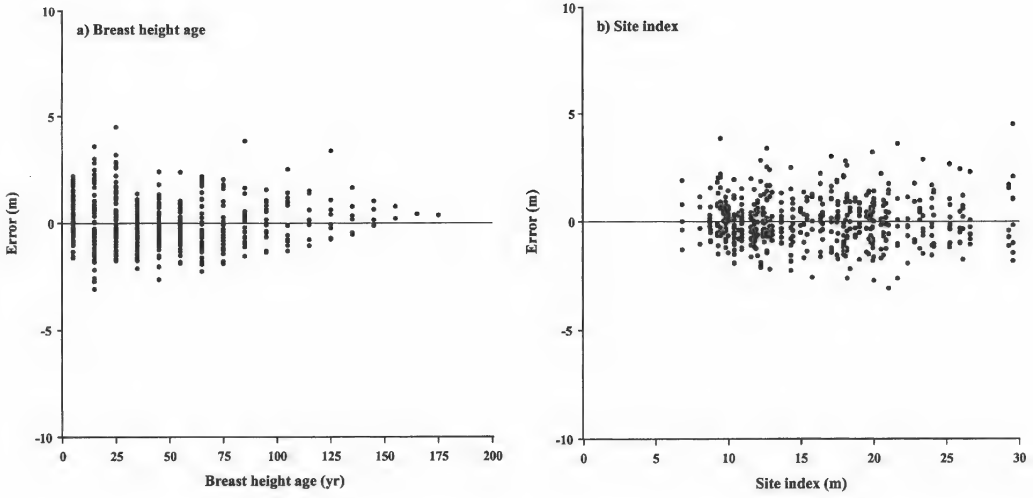


Figure 2. Residuals from the extended model plotted against breast height age (part a) and site index (part b). Note that the errors are weighted.

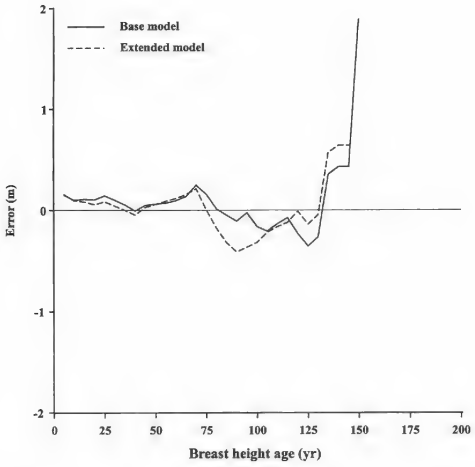
TABLE 5. Analysis of errors in height estimates by biogeoclimatic zone, and for all data combined for both fitted models. Mean errors that are significantly different from zero are indicated by asterisk.

Biogeoclimatic zone	Number of observations	Base model		Extended model	
		Mean error(m)	Std. dev.	Mean error (m)	Std. dev.
Boreal White and Black Spruce	384	0.1204	1.218	0.04979	1.219
Interior Cedar-Hemlock	111	0.1635	0.9260	0.6279*	1.064
Interior Douglas-fir	122	-0.1291	1.129	-0.2579*	1.174
Montane Spruce	102	0.05180	0.6127	-0.00007	0.7024
Sub-Boreal Pine-Spruce	32	0.2628*	0.6235	0.2430*	0.5309
Sub-Boreal Spruce	176	0.09701	0.6579	-0.1246*	0.6242
All	927	0.08565*	1.013	0.04659	1.061

provincial model developed by Huang et al. (1994). Because the upper range of the data for the Alberta Forest Service model was 90 yr, and the Huang et al. (1994) data did not extend much past 100 yr, we discontinued the comparison at 100 yr. The three models are plotted for site indices 10, 15, 20, and 25 m for comparison (Figure 4). We also plotted the mean error in estimated height and its 95% confidence interval by site index class (≤ 17.5 m and > 17.5 m) for the three models (Figure 5). The errors in estimated heights were calculated from the complete stem analysis data set at 5-yr age intervals from breast height age 5 to 100. There is little difference in height growth patterns to breast height age 100 for the base model and the Alberta Forest Service model (Figures 4, 5). Although the errors are significantly different from zero at some ages, in practical terms the difference is small. The Huang et al. (1994) model underestimated height below age 50 and overestimated height above age 50 at lower site indices. All three models fit well at higher site indices.

Discussion

Two new models are now available for estimating the height of trembling aspen growing in British Columbia from site index and breast height age. One model is a generic base model and the other is extended to be specifically calibrated for six biogeoclimatic zones.



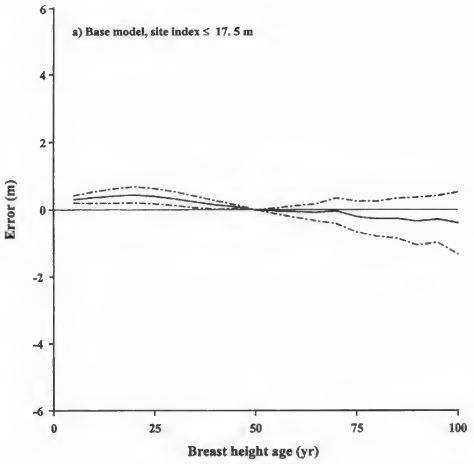


Figure 3. Mean error in the test data set plotted against breast height age for the two fitted models.

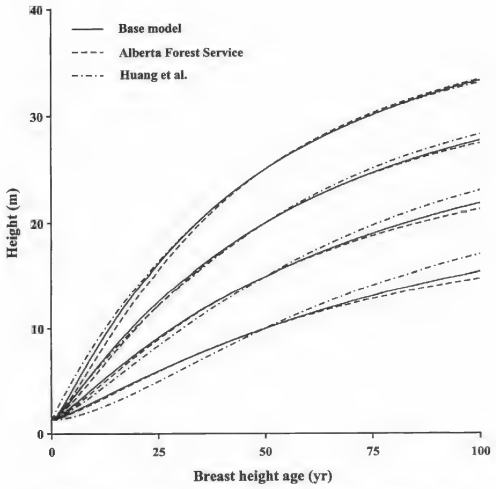


Figure 4. Graphical comparison of the base model, the current model for British Columbia (Alberta Forest Service 1985), and the provincial model by Huang et al. (1994). Curves for site indices 10, 15, 20, and 25 m are shown.

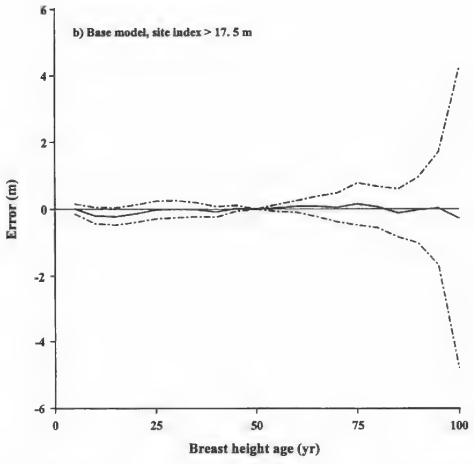
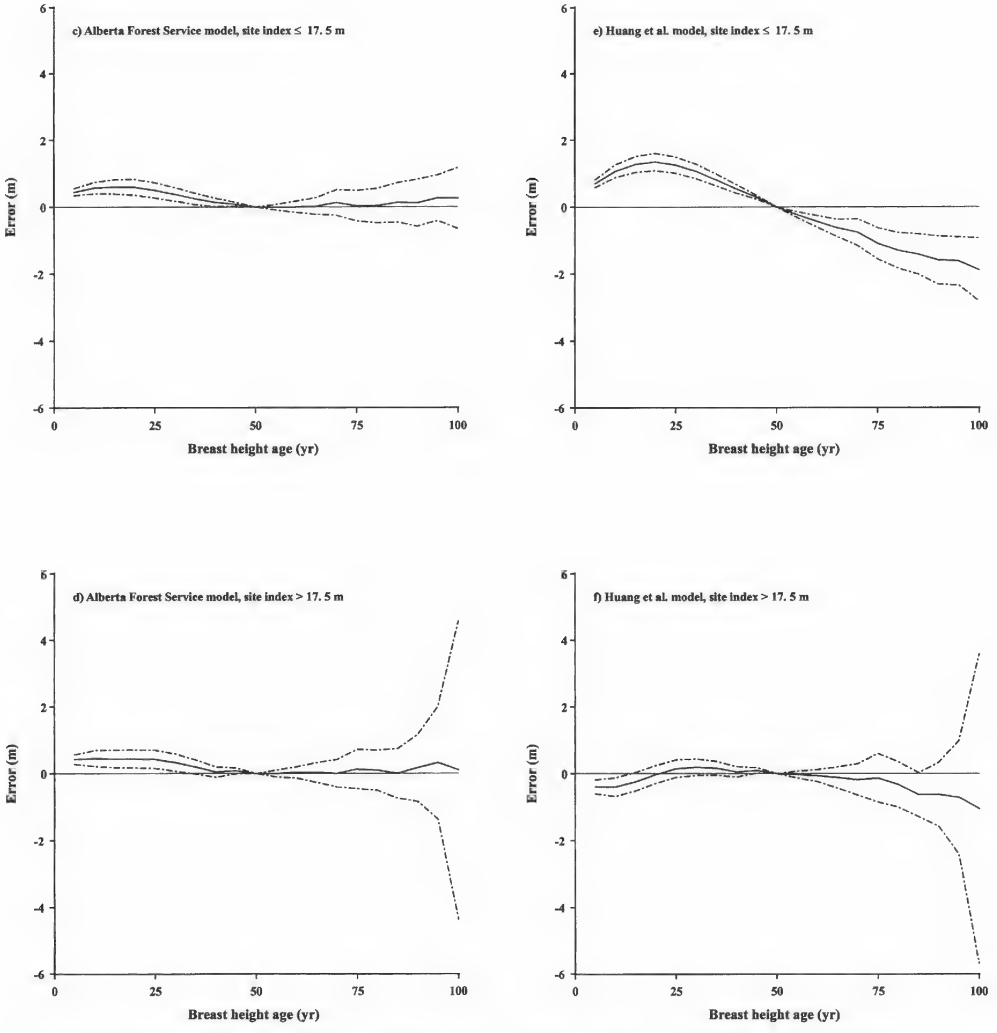


Figure 5(a–f). Mean errors and their 95% confidence intervals for

The trends in the site indices for the six biogeoclimatic zones (Table 2) sampled in this study correspond to the trends in their climate (Table 6). The ICH zone is the second-most productive zone in Canada (Meidinger and Pojar 1991), so that the high site indices are not surprising for that zone. In fact, the maximum height of 37.5 m recorded in one study stand in the ICH zone (Table 2) is greater than the 36.5 m previously observed on the best sites (Perala 1990). Compared to the other study zones, the ICH zone is influenced by the warmest and wettest cool temperate climate. Aspen site index gradually increased from 13.7 m in the BWBS zone to 15.1 m in the SBPS zone to 16.5 m in the SBS zone to 17.2 m in the IDF zone and to 22.2 m in the MS zone (Table 2). This trend is reflected in the tem-


c) Alberta Forest Service model, site index ≤ 17. 5 m
e) Huang et al. model, site index ≤ 17. 5 m
d) Alberta Forest Service model, site index > 17. 5 m
f) Huang et al. model, site index > 17. 5 m
Error (m)
Breast height age (yr)

the base model, the Alberta Forest Service model, and the Huang et al. (1994) model, by site class (≤ 17.5 m, > 17.5 m).

perature and growing season duration (increasing potential evapotranspiration), i.e., the number of months with the mean temperature >10°C, which increases from the BWBS zone to the SBPS zone to the SBS zone to the IDF zone. The MS zone, however, has a lower mean annual temperature and more months with a mean temperature >10°C than the IDF zone, but has higher mean annual precipitation, which could compensate for lower temperature and result in higher actual evapotranspiration. Although the MS zone has a lower mean annual precipitation, it has a higher mean annual temperature and slightly longer growing season than the SBS zone.

The base and extended models are graphed for site indices at 10, 15, 20, and 25 m (Figure 6). There were only 13 plots older than 120 yr breast height age, so the curves in Figure 6 are not well supported above this age. For some biogeoclimatic zones, the data are exhausted well below this age

TABLE 6. Environmental characteristics of the six biogeoclimatic zones.

Zone	Environmental characteristics		
	MAP (cm)[1]	MAT (°C)[2]	T>10 (mo)[3]
Boreal White and Black Spruce	45	-1.4	3
Interior Cedar-Hemlock	80	6.9	5
Interior Douglas-fir	44	4.3	5
Montane Spruce	60	3.2	4
Sub-Boreal Pine-Spruce	48	0.4	3
Sub-Boreal Spruce	65	3.3	3

[1]MAP – mean annual precipitation
[2]MAT – mean annual temperature
[3]T>10 – number of months with mean temperature > 10°C

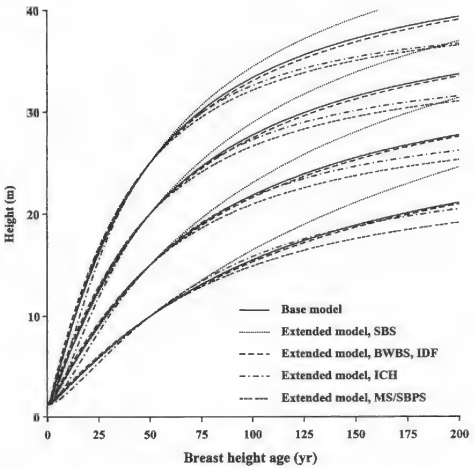


Figure 6. Height estimates from the base and extended models plotted against breast height age for site indices 10, 15, 20, and 25 m.

(Table 2), which must be considered when comparing and using the models. The largest difference in the height estimates between the models are above age 120. The base model, therefore, is adequate for all the zones, but the extended model would be preferred if the situation allows for its use. The adequacy of the base model is also borne out by the error analysis, where it performed about the same as the extended model (Table 5). The base model had a smaller mean error than the extended model in four of the six zones. The overall error for the base model was slightly larger than that for the extended model, but the difference was a matter of a few centimetres. Both models have about the same error across the range of breast height ages (Figure 3). In fact, the base model appears to have a smaller mean error in the 50-100 yr age range, which may be the most important ages because the rotation age for aspen can be between 60 and 90 yr total age (Peterson and Peterson 1995).

The SBS curves are conspicuous by their continued height growth at older ages, which could be attributed to a combination of climatic and edaphic factors. First, most of the aspen stands sampled in the SBS zone were associated with fine-textured, base-rich Luvisols (Krestov et al. 2000), which support productive aspen growth across its range (Perala 1990). Second, decay in relatively short-lived aspen is generally slower in cooler (boreal) climates, such as in the SBS zone, than warmer (temperate) climates (Perala 1990). More data are required to confirm whether the height growth pattern in the SBS zone is indeed different from the other zones. One plot in the SBS was older than 120 yr breast height age, so that the model is not well-supported at ages above 120 yr for this zone. However, the difference in the height growth trend starts before age 120 where the model is supported by more data. There is no evidence of bias in the model below age 120, indicating that the trend is not necessarily an artifact of one plot causing bias in the model.

In contrast, the plots from the ICH and the MS zones were the most productive, that is, they had the highest site indices. The plots from these two zones, however, had the lowest height trajectories, which could be due to perhumid (water surplus) and warm climate, especially in the ICH zone (Perala 1990), or perhaps to the low age range of the data from these zones or to some unknown biological factor. In the early growth stages and in closed-canopy stands, aspen develops a relatively narrow, short, pyramidal crown with a distinct apical dominance. In the late growth stages, crowns become domed. We hypothesize that the development of a flat, domed crown is associated with the onset of decline in height growth that may be environmentally or genetically triggered.

Four groups of biogeoclimatic zones had similar height growth patterns: SBS, BWBS/IDF, ICH, and MS/SBPS. It appears that, to some extent, these patterns could be related to climate, such

as for the SBS and ICH zones, but not the patterns of BWBS/IDF and MS/SBPS zone groups, which are climatically dissimilar. Given the unbalanced nature of the data set with respect to age, the similarity of all the curves (except for the SBS zone), and the inconclusive nature of the model testing, we are hesitant to conclude that we detected real differences in growth patterns, even though they were detected statistically in the model calibration.

The extended height-age model specific to the six biogeoclimatic zones should be used for sites in those zones. If the zone is unknown, or the site is in another zone, then the base model should be used. The differences between the zones when using the extended model can be significant, depending on the application, even though the curves look quite similar (Figure 6). As an example, we compare the models for the ICH and the BWBS zones with the following three scenarios.

1. At breast height age 15 and site index 10 m, the estimated heights are 3.43 m (ICH) and 4.23 m (BWBS). At site index 20 m, these estimates are 9.55 m and 11.53 m. Therefore, with the extended model, the difference in heights can be between 1 and 2 m.
2. In British Columbia, a harvested stand usually has to reach green-up height (often 3 m) before an adjacent stand can be harvested. For site index 10 m, the green-up age for aspen in the ICH zone is 13 yr and the green-up age in the BWBS is 9 yr. At site index 25 m, the green-up ages are 12 and 9.5 yr. Since green-up constraints are modelled in timber supply analyses, these differences could be significant for management units where the constraints are tying up timber.
3. Assuming a site has a height of 4 m at age 15 yr, the site index for sites in the ICH will be 12 m and the site index for sites in the BWBS will be 9.5 m. This 2.5 m difference in site index could translate into a significant amount of volume at rotation age.

Further to these examples, as one reviewer pointed out to us, height is critical in growth and yield modelling and small changes at young ages may result in significant changes in stand development in the model.

Acknowledgements

We thank British Columbia Forest Service staff from the Fort Nelson, Dawson Creek, Fort St. James, Mackenzie, and Morice Forest Districts for assistance in locating stands suitable for this study and for providing cutting permits. D. New, D. Brisco, B. Collins, D. Affleck, and K. Zidek from the University of British Columbia assisted with the sampling and sample preparation. R. Kabzems (British Columbia Forest Service) provided vegetation and environmental data for some plots. Funding for this project was provided by Forest Renewal British Columbia. P. Marshall, Forest Resources Department, University of British Columbia, provided review comments.

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Received 25 October 2001
Accepted for publication 4 April 2002

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Marko Manoukian and **Clayton B. Marlow,**[1] Animal and Range Sciences Department, Montana State University, Bozeman, Montana 59717-2900

Historical Trends in Willow Cover Along Streams in a Southwestern Montana Cattle Allotment

Abstract

Concern over the apparent scarcity of tall willows prompted changes in livestock grazing management in a southwestern Montana mountain valley to avoid degradation of riparian and aquatic habitats. We assessed potential improvement in the abundance of tall willows following implementation of a new management strategy by determining the effect of historic grazing patterns on willow canopy along streams within the USDA Forest Service grazing allotment. Willow canopy cover by stream reach was measured from air photos taken in 1942, 1965, and 1987. Cover from each year was compared for change over the 46-yr record. Willow canopy cover fluctuated along the streams in the allotment, but the general trend was upward from 1942 to 1987. Willow stem population demography was evaluated to ascertain whether historic grazing patterns had affected stem replacement. Stem age classes were normally distributed with a replacement cycle similar to those reported in other areas of the western United States and Canada. These data sets suggest that extended periods of rest (> 3 yr) are not necessary for willow recovery if livestock or wildlife use is closely controlled.

Introduction

The contribution of woody vegetation to the proper function of riparian areas has been recognized since the 1970s (Meehan et al. 1977, Jahn 1979). As awareness of the importance of woody species grew the Western Division of the American Fisheries Society published a position statement calling for the immediate application of best management practices to maintain riparian stream ecosystems to perpetuate the quality of western streams for fish, wildlife, and general recreational use (Western Division of the American Fisheries Society 1980). Even though public agencies and private landowners moved to implement best management practices following published guidelines (Chaney et al. 1990, USDI Bureau of Land Management and USDA Forest Service 1994), the results have recently been criticized as inadequate (Fleischner 1994, Belsky et al. 1999). Part of the reason for the slow or limited improvements noted by these authors may be our incomplete understanding of how woody riparian species respond to livestock grazing.

Even though willows and cottonwoods are the most common woody riparian species in the western United States (Mitsch and Gosselink 1986), there was, and is, relatively little information about how much grazing these species can withstand without becoming decadent (Thomas et al. 1979). Although four of the reports published prior to 1990 (Behnke and Raleigh 1979, Knopf and Cannon 1982, Rinne 1985, Elmore and Beschta 1987) made no mention of appropriate browsing levels, they consistently recommended 3-12 yr of complete rest for the recovery of heavily grazed willows. Schulz and Leininger (1990) reported that even though willow density inside and outside of a grazing exclosure was similar, the willows protected from grazing for 29 yr had 8 times the canopy cover than those in the grazed area. This led to their recommendation of at least 5 yr of rest from grazing to initiate willow recovery. However, Kovalchik (1991) reported that certain willow species turned over or replaced portions of their stem population every 15-18 yr. This meant that a large proportion of willow stems could die at any time during a rest period, which would require extension of the nongrazing treatment to achieve management goals. Taken in total this information suggested few management options other than to exclude livestock grazing for a decade or more. Elmore and Beschta (1987) cautioned managers and landowners to avoid the temptation to relax management prescriptions at the conclusion of the rest treatment or risk the loss of improvements gained during the livestock exclusion period.

These management recommendations were met with considerable resistance by livestock producers because of the potential for substantial

[1]Author to whom correspondence should be addressed.
E-mail: cmarlow@montana.edu

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reduction in livestock grazing opportunities on public lands during the initial recovery effort. Many public land grazers felt that prolonged periods of nonuse could be avoided with more detailed information on willow or cottonwood response to intensive grazing management.

The implementation of a new allotment management plan specifically to protect and enhance willows on a USDA Forest Service (USFS) cattle allotment in the Centennial Valley of southwestern Montana provided a timely opportunity to evaluate the proposals made by livestock grazing interests and to add to the information base on woody riparian species. The intense interest in protecting both riparian woody species and public land grazing demanded field methods that could separate changes in willow cover and regeneration caused by historic grazing patterns from those produced under the new grazing prescription (Knopf and Cannon 1982, Rinne 1985). Because early USFS monitoring efforts concentrated on upland plant communities, we had to reconstruct the effect of previous livestock grazing on the willow community in the Long Creek Cattle Allotment from a series of aerial photographs. We based our analysis on the information available in 1990 when the allotment management plan was amended. We hypothesized that analysis of aerial photos would indicate that the fragmentation of willow canopy cover along the streams in 1965, when the rest rotation grazing system was implemented, would be little different from that along the same streams in 1987 because of insufficient (< 10 consecutive years) rest from grazing.

Study Area

The Long Creek Cattle Allotment of the Beaverhead National Forest is located on the Centennial Divide, ~71 km southeast of Dillon, Montana (Figure 1). The allotment encompasses nearly 2200 ha, annual precipitation averages 480 mm, and elevation is ~2300 m (Caprio et al., 1994). Upland vegetation is within the big sagebrush/Idaho fescue (*Artemisia tridentata/Festuca idahoensis*) habitat type (Mueggler and Stewart 1980). Riparian vegetation is dominated by Geyer willow (*Salix geyeriana*), Booth willow (*S. boothii*), sedges (*Carex* spp.), and Kentucky bluegrass (*Poa pratensis*). Mature plants of both willows in the study area normally occur as multi-stemmed shrubs > 3 m tall.

The area has a record of combined sheep, horse, and cattle grazing since the turn of the century. Unrestricted grazing prior to 1935, coupled with custodial management until 1962, necessitated rangeland renovation and the implementation of

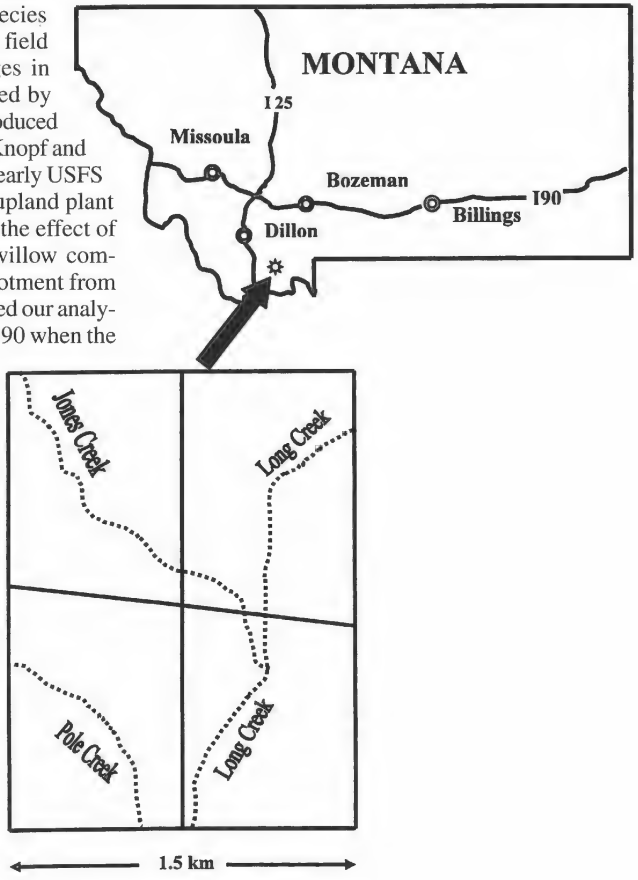

Figure 1. The location of the USDA Forest Service Long Creek cattle allotment in southwestern Montana. Pastures served as replicates in analysis of changes in willow canopy cover from 1942 to 1987.

grazing control practices to reverse an apparent downward trend in ecological condition of the uplands. As part of the renovation effort herbicide was applied in 1963 and 1964 to reduce the abundance of mountain big sagebrush (*Artemisia tridentata vaseyana)*. This action was followed by extensive cross fencing to facilitate the implementation of a rest-rotation grazing system. The allotment was divided into four grazing pastures to allow one pasture to be left ungrazed (rested) each year to promote recovery of upland plant communities (Figure 1). To provide water for livestock, the fencing design incorporated reaches of Pole Creek, Jones Creek, and Long Creek. Consequently, each of the four pastures in the Long Creek Cattle Allotment had stream reaches with similar riparian vegetation composition (Figure 1).

Control of grazing was enhanced by coupling a lower stocking rate (number of cattle for a specific period) and a shift in grazing season (from 1 June - 31 October to 16 July - 15 October) to the construction of the four pastures. These actions appeared to arrest the downward trend in ecologic condition until 1986 when the livestock permittee voluntarily reduced livestock numbers from 800 cow/calf pairs to 600 because of an increase in sagebrush cover. Shortly after that decision was made, USFS personnel concluded that the tall-willow (plants greater than 1.8 m in height) component of the allotment's riparian zone had declined. The perceived decline heightened management concerns because fragmented willow canopy cover could lead to decreased streambank stability, higher water temperature, and degraded riparian and aquatic habitats (Platts 1991, Fleischner 1994). To reverse the perceived fragmentation of the tall willow community and thereby avoid potential riparian and aquatic degradation, the USFS proposed that the recent livestock reduction become permanent. The permittee opposed the long-term reduction, but was willing to work with USFS to amend the existing grazing management plan to extend the scheduled rest period for each pasture to 2 yr. In return the permittee requested that an outside party, the Montana Agricultural Experimentation Station, monitor the response of the willow community to the longer rest period. This provided the opportunity to contrast the extent of willow cover along streams under custodial livestock management (1942 to 1965) to that under rest rotation grazing management (1965 to 1987).

Methods

Willow Canopy Cover

Three sets of aerial photographs spanning a 46-yr period were used to determine the change in willow canopy cover along the three main streams in the Long Creek Allotment. Aerial photographs from 1942 were purchased from the National Photographic Archives, Atlanta, Georgia and photographs taken in 1965 and 1987 were purchased from the Natural Resource Conservation Service Air Photo Field Office, Salt Lake City, Utah. Photographs were ordered at an enlarged scale of 1 cm = 121.92 m.

The photo scale was checked with a topographic map and recognizable landscape features. Clear 22 x 28 cm acetate sheets were placed on individual photos, covering the length of each stream within a pasture. Because each of the four allotment pastures had a stream, tall willow communities, and received a common treatment (rested one year in four), the pastures were treated as replicates for statistical analyses. This necessitated delineation of pasture boundaries on each set of acetate sheets. The area occupied by willows along each stream reach was traced onto the acetate sheets. Apparent breaks in willow canopy cover were identified and marked on the acetate sheets. A standardized dot grid template, 100 dots per 1.2 cm^2, was then placed over the acetate sheets. The number of dots within the outlined willow area and number of dots touching willows were totaled for each canopy cover break (Tueller 1977). The total number of dots was divided into the number of dots touching willows to approximate percent canopy cover. However, because a single canopy measure for each pasture would provide little information on fragmentation of the tall willow community cover, estimates were then stratified into five cover classes (Daubenmire 1959). Stratifying the canopy cover measures into cover classes allowed us to approximate willow canopy cover fragmentation over the period the allotment was under rest rotation grazing management. Because none of the canopy cover breaks measured on the aerial photographs had $\geq$ 75% canopy only cover classes 1 (0-5%), 2 (5-25%), 3 (25-50%), and 4 (50-75%) were used.

To compare canopy cover fragmentation along streams within a given year, and to estimate canopy cover changes over the 46-yr period, we determined

the percentage of the stream reach within each pasture that was occupied by each canopy cover class. The percentage of stream falling within each of the four cover classes was determined by placing a new set of acetate sheets over each set of aerial photographs. The stream channel, breaks in the canopy cover, and the associated cover classes were marked onto these acetate sheets. The length of stream within each cover class was measured by a digitizer, using the Sigma Scan 3.10 program. Sigma Scan was calibrated to the scale of the photographs by tracing a known distance with an electronic pointer on an electronic pad. The pointer and pad were used to measure total length of each stream from the stream channel acetate sheets. Stream channels were re-measured on photos from 1942, 1965, and 1987. The total length of individual cover classes was also measured from stream channel acetates. Stream length occupied by individual cover classes was divided by the total stream length. This calculation represented the percentage of stream occupied by the individual cover classes. Changes in the percent of stream reach occupied by each cover class over time were used as the primary indicator of willow canopy cover fragmentation.

Stem Age

In 1991, we selected five locations, evenly distributed along the length of streams in each of the four pastures, as collection sites for willow stems. Two average size willows, one each of Geyer and Booth, were collected for stem aging at each location. Individual willows were chosen based on comparable height and diameter with other willow clumps at the location.

The base of each willow was measured with a 2-m ruler along a north-south axis. Five stems equally spaced along each axis were selected for removal. Each stem was cut at ground level. Stems were shortened to 20 cm, permanently tagged, and transferred to the lab. The narrowest diameter of each stem was measured to the nearest millimeter.

The end of the stem closest to the ground was shaved with a sharp knife to produce a smooth surface and dipped in water to accentuate growth rings. Annual growth rings were counted under a 1 x 10 binocular microscope. We analyzed 195 stems, 50 each from Long Creek, Jones Creek, and Lone Butte Pastures. Fifty stems were also collected from Pole Creek Pasture, however, five stems were lost resulting in only 45 for Pole Creek Pasture. Due to the turnover rate of willow stems within a willow clump, these data do not indicate the age of the original root crown but rather the clonal stem. For this reason, cross dating was not required. Multiple regression analyses were used to determine the correlation of species and diameter on stem age by pasture. Correlation analysis ($P = 0.05$) was then used to determine the relation between stem diameter and stem age for all 195 stems.

Data Analysis

A one-way ANOVA was used to test differences between the four canopy cover classes within each year (n = 4). The same statistical procedure was also used to test for differences in each cover class among years (n = 3). Pastures were used as replicates with $P = 0.05$ set for determining significance. Mean separation was performed with a least significant difference test.

Results

Willow Canopy Cover

In 1942, the distribution of the various willow canopy cover classes along the three streams flowing through the allotment appeared to be relatively uniform (Table 1). After 23 yr of custodial management (1942-1965) the percent of stream reaches occupied by the smallest and largest cover classes had declined while those reaches covered by willow canopies of 5-25% and 25-50% had increased. In 1965 the difference in stream reaches with more than 50% willow canopy cover and those with lesser amounts was not significant ($P = 0.07$)(Table 1).

TABLE 1. The percent of stream reach within the Long Creek allotment covered by various willow canopy cover classes in 1942 (custodial management-no rest from grazing), 1965 (initiation of rest-rotation grazing management) and 1987 (22 years of rest rotation grazing management). Values with the same superscript letters in 1987 are not significantly different at P=0.05.

	Percent Willow Canopy Cover			
Year	<5	5-25	25-50	50-75
1942	35	24	16	28
1965	29	33	38	1
1987	24[a]	15[a]	57[b]	6[a]

After 22 yr of rest rotation grazing management (1965-1987) there were significantly more ($P = 0.02$) stream reaches with a willow canopy cover of 25-50% than any other cover class (Table 1). When the percent of stream reaches covered by each cover class in 1942 was compared with the same measure in 1987, reaches with 25-50% canopy had increased but not to a significant level ($P = 0.06$), while none of the other cover classes changed significantly during the same period.

Stem Age

No significant correlation existed between species and stem age, and between pasture and stem age. Therefore, all stem data were pooled and are presented as an allotment average. The individual willows sampled contained a wide distribution of stem ages (Figure 2). While certain age classes were absent from some pastures, the sampled population within the allotment was represented in all age classes from 1 yr to 19+ yr. Only Jones Creek had two consecutive years with no apparent stem production. Stem age averaged 9.5 yr on the allotment and fewer than 13% of the collections were >14 yr old. Additionally, the correlation between stem diameter and stem age for all 195 stems was significant ($P < 0.0001$, $r^2 = 0.63$), indicating that larger diameter stems were older than smaller stems.

Discussion

According to the extensive review of riparian literature by Fleischner (1994) and Belsky et al. (1999) the willow canopy along the streams in the Long Creek allotment should have declined and become fragmented because of the allotment's long history of livestock use. However, analysis of a series of aerial photographs of the allotment from 1942 to 1987 did not reveal the expected fragmentation of the willow community. The nearly uniform distribution of willow canopy classes along the allotment's three streams in 1942 served as an effective baseline for establishing the trend in

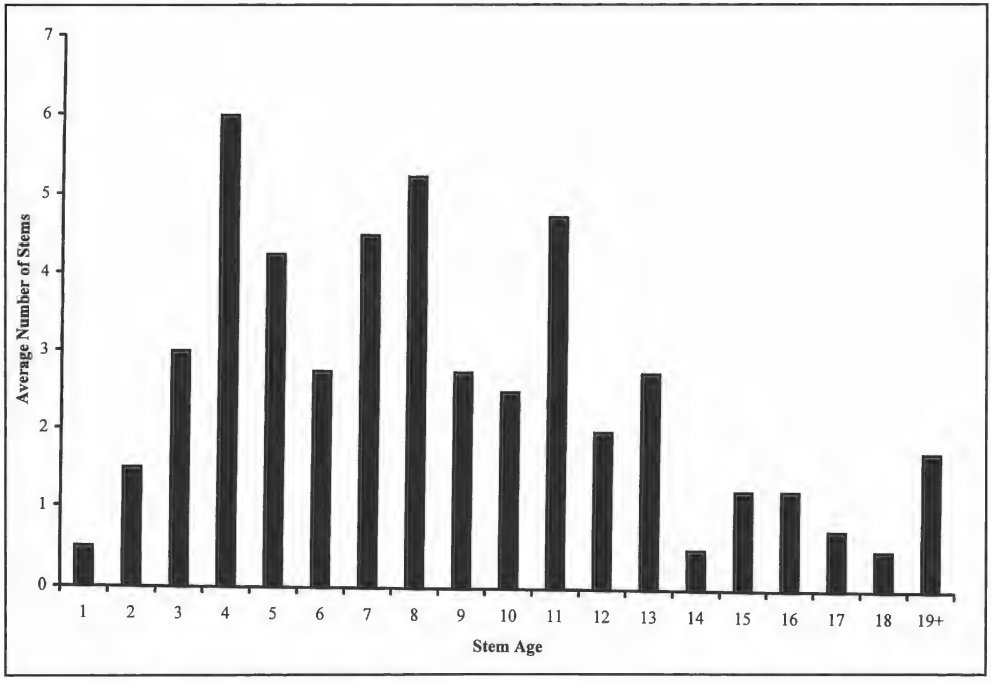

Figure 2. The stem age class distribution developed from collections made from randomly selected willows in the USDA Forest Service Long Creek allotment.

willow canopy with and without rest from grazing. There is little evidence that the Long Creek allotment received any rest from grazing from 1942 to 1965, yet willow canopy cover remained relatively static (Table 1). This pattern would be expected if the willow community had been in high ecological condition (Knopf and Cannon 1982), but historic livestock records suggest that willow condition in the Long Creek allotment in 1942 should have been relatively low. The relative increase in stream reaches with 5-25% cover and 25-50% cover from 1942 to 1965 (Table 1) suggests that the lower stocking rates implemented under custodial management maintained willow canopy cover. However, this increase stands in stark contrast to the decline in the relative amount of stream reach with 50-75% willow cover (Table 1). While the apparent break up of the heavier willow cover could be attributed to livestock use, USFS records indicate that aerial spraying was conducted in 1962 and 1963 to control sagebrush in the uplands. The lack of riparian monitoring data from that period complicates efforts to determine whether livestock use or herbicide drift was responsible for the dramatic decline in proportion of stream reaches with > 50% willow cover. Nonetheless, the lack of a significant difference between stream reaches with cover classes 1, 2, and 3 at the beginning of the rest rotation grazing management system in 1965 compared to the significant difference (Table 1) between the same cover class distributions in 1987 indicate that year long rest was sufficient to initiate willow recovery. The change in the amount of stream reach with 50-75% willow canopy between 1965 and 1987 further suggests that willow recovery was unhindered under rest rotation grazing management. Further support for rejecting the study hypothesis arises from closer examination of the willow stem data.

Three lines of evidence indicate that rest rotation grazing management promoted willow stem recruitment. First, the stem-age population curve was fairly uniform with fewer than 13% of the stems older than 14 yr (Fig. 2). Second, skewed stem age groups indicative of heavy browsing use were absent. Third; the mean stem age (9.5 yr) was nearly identical to willows protected from grazing for 29 yr (Schulz and Leininger 1990).

The turnover rate of individual stems in the Long Creek allotment appears rapid, because 87% of the samples were <14 yr. Therefore, willow stem populations may have completely turned over three times during 1942 to 1991. A complete turnover of stems every 15 yr on the Long Creek Allotment is similar to stem senescence in Geyer and Booth willow at 15-20 yr in central Oregon (Kovalchik 1991). Begin and Payette (1991) suggested turnover occurred from 10-14 yr for planeleaf willow (*S. planifolia*) along a Quebec lakeshore. Consequently, it appears that cattle grazing during 1942 to 1987 did not affect natural turnover patterns and that individual willows could continue to produce replacement stems at a sufficient rate under rest rotation grazing to expand willow canopy cover.

While aerial photographs and willow stem age data did not provide information about the density or generation of new tall willow clumps within the Long Creek Allotment, streamside willow canopy cover generally increased (Table 1) and willow stem recruitment was similar to records from other areas in the west and northeast (Begin and Payette 1991, Kovalchik 1991). At first glance, the results of this study contradict the findings of Knopf and Cannon (1982) and recommendations that willows need extended rest periods to recover from overuse (Behnke and Raleigh 1979, Rinne 1985, and Elmore and Beschta 1987). However, in contrast to these management recommendations, the grazing management implemented on the Long Creek allotment included rest, reduced stocking rate, a shorter grazing season delayed until mid July, and sagebrush control. This management action follows the recommendation that careful control of the season and intensity of livestock use fostered improved riparian function (Elmore and Beschta 1987). Thus, our results corroborate rather than contradict the earlier grazing studies. Short rest periods (< 3 yr) are probably inadequate for willow recovery without concurrent changes in season and intensity of use.

Even though several authors (Kay and Chadde 1991, Kovalchik 1991, Singer 1996, and Belsky et al.1999) suggest that willows require extended rest periods to recover from heavy use by livestock or wildlife, the 46-yr photographic record of Long Creek indicates that long periods of nonuse can be avoided through close control of season and intensity of ungulate use. The photo record also supports the recommendation of Clary et al. (1996) that grazing practices might have to be in place for several decades before degraded riparian vegetation begins to improve.

Acknowledgments

We thank the Sheridan Ranger District, Beaverhead-Deerlodge National Forest, and the Koch Cattle Company, Dillon, Montana for the financial support that made this project possible.

We would also like to acknowledge Resource Concepts, Inc., Carson City, Nevada and Dr. John Lacey, former Montana State University Extension Range Specialist, for their advice and help with the study design.

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Received 6 February 2001
Accepted for publication 24 March 2002

B. J. Hawkins,[1] **R. S. Koppenaal,** Centre for Forest Biology, University of Victoria, Victoria, British Columbia, Canada, V8W 3N5

and

A. K. Mitchell, Pacific Forestry Centre, Canadian Forest Service, Victoria, British Columbia, Canada V8Z 1M5

Proximity to a Stand Edge Influences Growth of Advance and Planted Pacific Silver Fir Seedlings

Abstract

Growth and physiology of advance regeneration, present in the understory before harvest, and planted seedlings of Pacific silver fir were compared in three environments created by increasing distance from an edge of a montane clearcut on Vancouver Island, British Columbia, Canada. The objective was to quantify growth limitations and their underlying mechanisms in relation to light and nutrient availability. The site was clearcut in 1989. In 1993, plots were established 5-10 m inside the north-east facing stand edge, and 12-17 m and 60-65 m into the adjoining clearcut. Microclimate data were collected, and biomass allocation, specific leaf area, and net photosynthesis of advance and planted seedlings in the plots were measured in 1993. Height growth and foliar nitrogen concentration of advance and planted seedlings were measured over a 5 yr period.

Light and air temperature increased from the inside edge environment into the clearcut. Soil moisture did not differ greatly among environments. Seedlings of both regeneration types grew tallest in the clearcut, and specific leaf areas were lower in the clearcut. In 1993, root:shoot ratios and rates of net photosynthesis were greater in advance than planted seedlings. Planted seedlings were significantly taller than advance regeneration by 1998, 5 yr after establishment, however, this size difference was due mainly to the larger starting size of planted seedlings. By 1998, foliar nitrogen concentrations did not differ between regeneration types. Foliar nitrogen concentrations were low in all environments, which supports the contention that growth check of Pacific silver fir in montane clearcuts is associated with nitrogen deficiency.

Introduction

Pacific silver fir (*Abies amabilis*) grows in cool, moist, coastal forests from northern California (41°N) to southwest Alaska (56°N). In the central and southern part of its range, Pacific silver fir is restricted to montane forests above 300 m and 1000 m, but north of 50°N it can be found from sea level to the subalpine zone (~1400 m) (Pojar and MacKinnon 1994). In coastal British Columbia, montane forests containing Pacific silver fir, western hemlock (*Tsuga heterophylla*) and yellow cedar (*Chamaecyparis nootkatensis*) are projected to be the major source of timber for the next 40-60 yr (Canadian Forest Service 1994).

Regeneration requirements of montane forests are significantly different from those of low elevation coastal forests (Klinka et al. 1992). Historically, montane forest regeneration has been slow to establish in clearcuts and has often exhibited growth stagnation (Herring and Etheridge 1976). These problems may relate to a short growing season, low soil and air temperatures, nutrient deficiency of montane soils, or vegetative competition (Grier et al. 1981, Arnott and Beese 1995, Prescott 1997).

Concerns over ecosystem integrity and diversity, and aesthetic values have resulted in a move away from clearcut systems in coastal montane forests of British Columbia (Arnott and Beese 1997). Few studies have examined regeneration mechanisms under alternative silviculture systems in montane forests, but it is apparent that the increased edge created by partial cutting systems has implications for growth of seedlings. Forest edges, whether created by natural or artificial disturbance, moderate microclimatic extremes and create interactions between light, temperature, moisture, and nutrient availability that can modify seedling growth (Chen and Franklin 1992; Chen et al. 1995; Gray and Spies 1996, 1997; Mitchell 2001). Forest edges, therefore, provide an opportunity to study regeneration responses to gradients of resource availability.

Pacific silver fir is highly shade tolerant, and regenerates abundantly under mature stands (Klinka et al. 1992). Following stand harvest, these

[1] Author to whom correspondence should be addressed.
E-mail: bhawkins@uvic.ca

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naturally regenerated seedlings are referred to as advance regeneration. Several studies have examined the response of Pacific silver fir advance regeneration to microclimatic gradients created by forest edges. Leaf morphology and physiology change with gradients of light, temperature, and moisture created by clearcutting (Tucker et al. 1987), and growth of advance regeneration of Pacific silver fir and subalpine fir (*Abies lasiocarpa*) increases with irradiance (Klinka et al. 1992).

Pacific silver fir advance regeneration is often relied upon to reduce the risks and costs associated with plantation establishment on montane sites in British Columbia. While Pacific silver fir responds to release even after long periods of suppression (Klinka et al. 1992) and advance regeneration may outperform planted stock (Scagel et al. 1989), stocking and performance of advance regeneration is often a concern (Weetman and Vyse 1990, Green and Bernardy 1991). The shade-tolerant attributes that allow survival in the understory may be associated with prolonged acclimation periods and growth delays in advance regeneration following clearcutting (Herring and Etheridge 1976, Wagner 1980). Shade foliage morphology (Tucker et al. 1987) and shallow rooting habit (Herring and Etheridge 1976) may contribute to poor initial performance of advance regeneration. Nursery-grown container seedlings used for regeneration of montane sites differ from advance regeneration because they have higher foliar nitrogen concentrations and lower root:shoot ratios, and may respond differently to resource availability.

While many studies have examined growth of advance regeneration of Pacific silver fir, few have compared the performance of advance and planted seedlings. In this study, growth and physiology of advance regeneration were compared to planted seedlings of Pacific silver fir in three environments created by increasing distance from an edge of a montane clearcut on Vancouver Island. The objective was to quantify growth limitations and their underlying mechanisms in relation to light and nutrient availability.

Methods

The study site is located on eastern Vancouver Island (46° 55'N, 125° 25'W, 800 m) in the Coastal Western Hemlock (CWH) mm2 biogeoclimatic variant (Meidinger and Pojar 1991). Site aspect is N20°E on a 4° slope. The soil is a coarse loamy orthic humic podzol with a thick humus layer (14-40 cm). Mean air temperature on the site is 15.0°C in July and -1.0°C in January (Ross Benton, Pacific Forestry Centre, personal communication), and mean annual precipitation is > 1400 mm (Environment Canada, unpublished report, Campbell River Airport). Part of the old-growth stand on the site was clearcut in midsummer, 1989. Western hemlock, mountain hemlock, Pacific silver fir, and yellow cedar were the predominant overstory species, averaging 28 m in height.

In April 1993, three treatment environments were established: clearcut, 60-65 m from the northeast facing stand edge; outside edge, 12-17 m from the stand edge; and inside edge, 5-10 m inside the stand edge. Three replicate plots, 25 m × 5 m were established with their long axes parallel to the northeast-facing stand edge in each environment. The three replicates in each environment compensated for variation in microtopography across the site.

Within each treatment environment, 50 seedlings of Pacific silver fir advance regeneration < 50 cm in height were randomly selected across all replicates and tagged. An age of 10 ± 2 yr was determined for a sample of six advance seedlings of similar size in each environment which confirmed they were present in the understory prior to harvest. Forty 1-yr-old container seedlings of Pacific silver fir (PSB 313B 1+0) were planted at 1 m × 1 m spacing in each replicate plot.

From 4 June–29 September 1993, air temperature, photosynthetically active radiation (PAR), and soil water potential were measured every 10 min in each environment, an hourly average calculated and recorded with an Omnidata International Easylogger 900. Air temperature was measured at one location in each environment with shaded thermocouples 30 cm above the soil surface. PAR was measured at ground level with four LI-COR 190SA quantum sensors in both the inside and outside edge environments, and two sensors in the clearcut. Soil water potential at -10 cm was measured with soil matric potential blocks at one location in each environment. Over the 5 yr study, the relative ranking of the three treatment environments by temperature, light, and moisture conditions was consistent.

Height of the planted and advance seedlings was measured at the time of establishment in April

1993, and in September 1994 and 1998. In September 1993, six seedlings of both planted and advance regeneration were excavated in each replicate and analyzed for root and shoot dry mass and specific leaf area (SLA = leaf area/leaf dry mass).

Owing to differences in initial size between planted and advance seedlings and among advance seedlings in the three environments (Figure 1), 5 yr height was analyzed using analysis of covariance, with initial height as the covariate. Mortality and browse resulted in uneven sample sizes within regeneration types, and sample sizes differed among replicates for advance seedlings, thus analysis of variance was carried out using a general linear model (SAS Institute Inc. 1988). Means were compared with Tukey's means test. Height relative growth rate (RGR) between 1994 and 1998 was also calculated ([ln(height '98) – ln(height '94)]/4 yr) to examine growth rates independent of initial seedling size. A 4-yr period was chosen because planted seedlings were considered established after two growing seasons. RGR results were arcsine square root transformed and analyzed by ANOVA (SAS Institute Inc. 1988). The level of significance for all statistical analyses was $P \leq 0.05$.

Current-year needles were sampled for nitrogen concentration prior to planting in April 1993, in late September 1993 and 1994, and in November 1998. In September 1993, 60 seedlings per environment and regeneration type, 20 per replicate, were sampled and the foliage bulked by replicate and regeneration type. In 1994, 15 seedlings per replicate of each regeneration type were sampled individually. In 1998, five seedlings per replicate of each regeneration type were sampled. Foliage was oven dried at 80°C, ground to pass a 1 mm mesh sieve, and analyzed using the H_2SO_4-H_2O_2 digestion method and a Technicon autoanalyzer (Parkinson and Allen 1975). Foliar nutrient concentration data were arcsine square root transformed, and analyzed using analysis of variance (SAS Institute Inc. 1988).

Net photosynthesis (Pn) and transpiration (Et) rates were measured with a portable Leaf Chamber Analyser Type LCA-3 on 8 June, 19 July, 12 August, and 8 September 1993. Five or six randomly selected seedlings of each regeneration type in both the clearcut and outside edge environments were measured between 14:00 and 16:00 hr on the first three dates, and between 9:00 and 10:30 hr in September. Six seedlings in the inside edge environment were measured in July and September only. Xylem pressure potential was measured with a Model 3005 Plant Water Status Console immediately following the photosynthetic measurement for each seedling. Data were analyzed by ANOVA (SAS Institute Inc. 1988).

Results

Microclimate

The clearcut was exposed to 100% of full sun, and maximum daily PAR ranged between 400 and 2100 μmol m^{-2} s^{-1}. PAR in the outside edge environment averaged 84 ± 1.6% of that in the clearcut, and the maximum ranged from 350 to 1950 μmol m^{-2} s^{-1}. PAR in the inside edge environment averaged 18 ± 1.7% of the clearcut, and maximum PAR was below 400 μmol m^{-2} s^{-1} on most days.

Mean daily air temperature at 30 cm in the clearcut ranged from 5 to 18°C. Temperatures in the inside and outside edge environments were generally 1-4°C lower than the clearcut. Maximum air temperatures were 30.5°C in the clearcut, and 26.5°C and 21.5°C on the outside and inside edges. Minimum temperatures averaged 0.5-3°C lower in the clearcut and outside edge environments than the inside edge environment. Soil water potentials in the three environments differed by ≤ 0.005 MPa until mid-September, when a period of low rainfall resulted in soil water potential dropping to a low of -0.047 MPa in the inside edge and -0.028 MPa in the clearcut. During the September dry period, soil water potential remained at -0.02 MPa in the outside edge environment.

Survival, Growth, and Morphology

In 1998, 5 yr after establishment, survival of the advance seedlings selected for measurement was 70%, 98%, and 82% in the clearcut, outside edge, and inside edge environments. Five year survival of planted seedlings was 84%, 81%, and 86% on the clearcut, outside edge, and inside edge environments.

Analysis of covariance showed that the covariate, initial seedling height, had a significant (P=0.03) effect on 5-yr height. Both environment and regeneration type significantly (P<0.001) affected 1998 height, with the tallest seedlings in the clearcut, and the smallest in the inside edge (Figure 1). Planted seedlings were

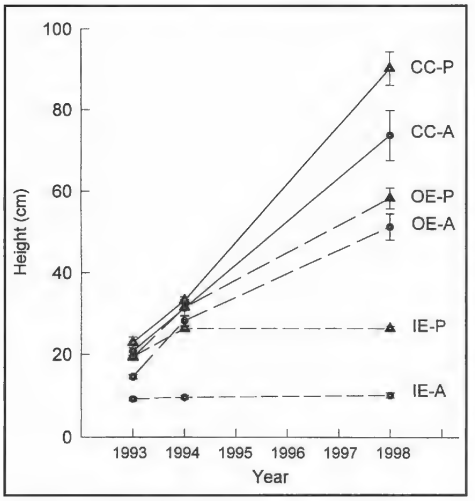

Figure 1. Mean (±S.E.) height of advance (A) and planted (P) regeneration of Pacific silver fir in clearcut (CC), outside edge (OE) and inside edge (IE) environments in year one, two, and five of the study

significantly taller than advance seedlings 5 yr after planting (Figure 1). The effect of replicate within environment was not significant in any of the analyses.

Analysis of 4-yr height RGR showed no significant difference between regeneration types, thus the effect of regeneration type on 1998 height was due to differences in initial size. Environment significantly affected height RGR ($P<0.001$). Height RGR was 0.16 ± 0.02 in the clearcut, 0.11 ± 0.01 in the outside edge, and -0.003 ± 0.05 in the inside edge environment. The negative RGR in the inside edge environment was due to the die-back of shoot tips in some seedlings.

Analysis of SLA in 1993 showed that planted seedlings altered foliar morphology in response to the different light environments in one growing season. SLA of both regeneration types was greatest in the edge environments and least in the clearcut. SLA of advance seedlings was 88.5 ± 2.5 $cm^2 g^{-1}$, 106.4 ± 4.1 $cm^2 g^{-1}$, and 101.2 ± 4.6 $cm^2 g^{-1}$ in the clearcut, outside, and inside edge environments. SLA of planted seedlings was 81.8 ± 9.7 $cm^2 g^{-1}$, 123.7 ± 7.4 $cm^2 g^{-1}$, and 152.7 ± 9.7 $cm^2 g^{-1}$ in the same environments. Dry needle weight of advance seedlings was greater than planted seedlings (0.54 ± 0.01 g/100 leaves vs. 0.35 ± 0.01 g/100 leaves). Dry needle weight of both regeneration types was greater in the clearcut than in the outside or inside edge environments (0.55 g/100 leaves, 0.41 g/100 leaves, and 0.38 g/100 leaves).

In 1993, mean root:shoot ratio of advance seedlings was 0.53 ± 0.05, significantly greater than planted seedlings (0.32 ± 0.01) ($P<0.01$). Root:shoot ratio of planted seedlings did not differ among environments, and one growing season after planting still reflected conditions in the nursery rather than the planting site. By 1993, advance seedlings in the outside edge and clearcut had three growing seasons to respond to changed conditions created by overstory removal. Root:shoot ratio of advance seedlings differed among environments and was 0.77 ± 0.08 in the inside edge, 0.43 ± 0.05 on the outside edge, and 0.41 ± 0.03 in the clearcut. No further biomass sampling was conducted after 1993 due to the difficulties of seedling excavation.

Foliar Nutrients

Prior to planting, foliar nitrogen concentration of five container seedlings averaged $1.8 \pm 0.09\%$. We assumed that prior to harvest, foliar nitrogen concentrations of advance regeneration were similar to inside edge seedlings in 1993, about 0.8%. In September 1993, one growing season after planting and four growing seasons after harvest, foliar nitrogen concentration of current-year needles had declined to less than 1.2% in all planted seedlings, but was greater than 1.2% in advance seedlings in the clearcut and outside edge (Figure 2). There was a significant interaction between environment and regeneration type in foliar nitrogen concentration ($P<0.05$). Foliar nitrogen concentration was greatest in advance seedlings in the high-light clearcut and outside edge environments, while nitrogen concentration in planted seedlings was highest in the inside edge (Figure 2).

In 1994, the environment x regeneration type interaction was still significant in the analysis of nitrogen concentration of current-year needles ($P<0.0001$). Foliar nitrogen concentration was greatest in planted seedlings in the clearcut and in advance seedlings in the outside edge, but not significantly different between regeneration types in the inside edge (Figure 2). On average, nitro-

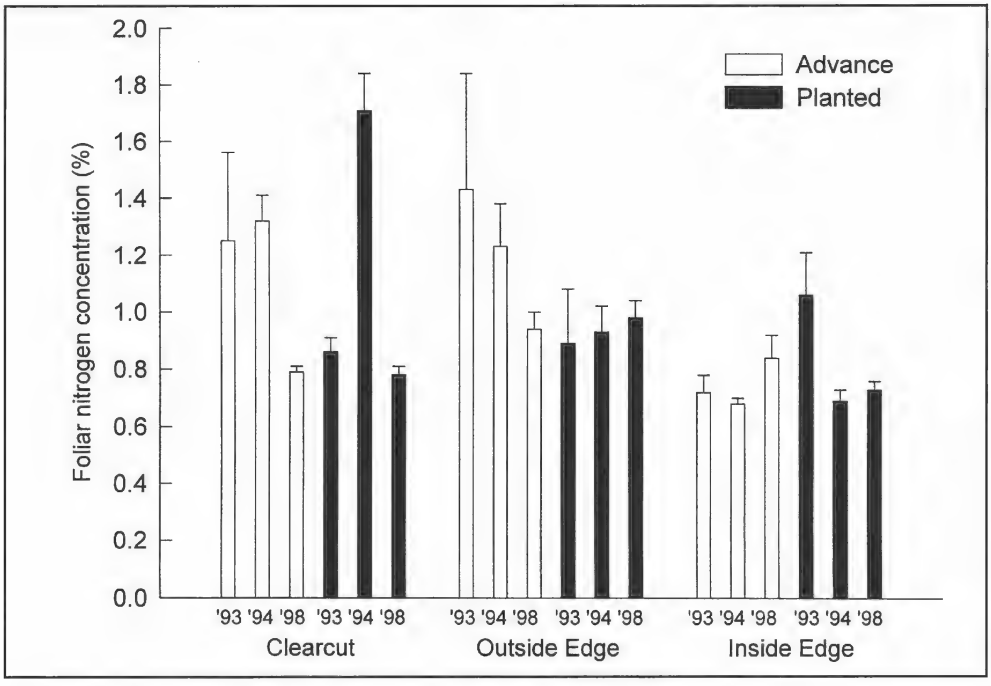

Figure 2. Mean (±S.E.) nitrogen concentration of current-year needles of advance and planted regeneration of Pacific silver fir in three environments in year one, two, and five of the study

gen concentrations were greatest in the clearcut and lowest in the inside edge seedlings.

In 1998, environment was the only significant effect in the analysis of nitrogen concentrations of current-year needles ($P<0.005$). Nitrogen concentrations were greatest in needles of seedlings from the outside edge, but were not significantly different between the clearcut or inside edge environments (Figure 2).

Net Photosynthesis and Water Relations

Over the first growing season Pn and Et of advance regeneration in the clearcut and outside edge environments were consistently higher than those of planted seedlings, except on 8 June which was a cool, overcast day (Table 1). Within each regeneration type, Pn and Et were not significantly different between the clearcut and outside edge environment, except on 8 September when the shade from the stand edge eclipsed the outside edge replicates by the time of measurement (Table 1). On average, however, Pn was greatest in the clearcut. In the low light environment of the inside edge, Pn was very low in advance seedlings, and negative in planted seedlings (Table 1).

Xylem pressure potentials were not significantly different among environments or regeneration types on two of the four measurement dates (Table 1). On 19 July and 8 September, xylem pressure potentials were significantly lower in the clearcut seedlings compared to the outside edge seedlings ($P<0.05$). On 8 September, planted seedlings in the outside edge replicates had significantly lower xylem pressure potentials than advance seedlings (Table 1).

Discussion

Biological responses at forest edges are influenced not only by distance from the edge, but also by edge orientation, patch size and shape, and topographical features, among other variables (Chen and Franklin 1992). We assessed the interactions between climatic factors and seedling growth intensively at one site by studying how the edge

TABLE 1. Mean (± S.E.) rates of net photosynthesis (Pn–μmol m^{-2} s^{-1}) and transpiration (Et–mmol m^{-2} s^{-1}), and xylem pressure potential (ψ–MPa) of advance and planted Pacific silver fir seedlings in three environments on four days over the growing season. Means followed by the same superscripted letter are not significantly different within sampling date.

			Advance			Planted		
Date	Parameter		Clearcut	Outside Edge	Inside Edge	Clearcut	Outside Edge	Inside Edge
8 June	Pn	(n=5)	3.71 (0.4)^{a}	3.29 (0.4)^{a}	-	4.56 (0.3)^{a}	3.87 (0.2)^{a}	-
	Et	(n=5)	1.71 (0.1)^{b}	1.56 (0.1)^{b}	-	2.64 (0.3)^{a}	2.27 (0.2)^{a}	-
	ψ	(n=5)	-0.73 (0.0)^{a}	-0.77 (0.1)^{a}	-	-0.73 (0.1)^{a}	-0.69 (0.1)^{a}	-
19 July	Pn	(n=6)	2.92 (0.4)^{a}	2.71 (0.3)^{a}	0.56 (0.3)^{c}	1.04 (0.5)^{b}	1.03 (0.1)^{b}	-2.67 (0.9)^{c}
	Et	(n=6)	2.61 (0.2)^{a}	2.46 (0.2)^{a}	0.91 (0.1)^{b}	1.05 (0.1)^{b}	0.97 (0.0)^{b}	1.27 (0.3)^{b}
	ψ	(n=6)	-1.10 (0.0)^{a}	-0.86 (0.1)^{b}	-0.83 (n=2)	-1.07 (0.1)^{a}	-0.70 (0.1)^{b}	-0.77 (n=2)
12 Aug.	Pn	(n=5)	4.19 (0.4)^{a}	3.15 (0.5)^{a}	-	1.82 (0.4)^{b}	0.89 (0.4)^{b}	-
	Et	(n=5)	2.32 (0.2)^{a}	1.74 (0.1)^{b}-	-	1.09 (0.1)^{b}	1.43 (0.4)^{b}	-
	ψ	(n=5)	-1.25 (0.1)^{a}	-0.96 (0.1)^{a}	-	-1.05 (0.1)^{a}	-0.89 (0.1)^{a}	-
8 Sept.	Pn	(n=6)	3.47 (0.6)^{a}	0.60 (0.6)^{b}	0.07 (n=2)	2.56 (0.7)^{a}	0.63 (0.4)^{b}	-0.71 (n=2)
	Et	(n=6)	3.57 (0.2)^{a}	2.49 (0.2)^{b}	0.61 (n=2)	1.77 (0.2)^{c}	1.16 (0.2)^{c}	0.77 (n=2)
	ψ	(n=6)	-1.34 (0.0)^{a}	-1.00 (0.1)^{b}	-0.81 (n=2)	-1.18 (0.1)^{ab}	-0.68 (0.1)^{c}	-0.60 (n=2)

environments modified photosynthesis, nitrogen acquisition, and growth processes over 5 yr.

A gradient of increasing light and increasing temperature existed from the inside edge environment to the outside edge and clearcut environments. Increased light and temperature can both result in greater rates of net photosynthesis and growth. The estimated light saturation point for Pacific silver fir is as low as 650 μmol m^{-2} s^{-1} (Mitchell and Arnott 1995) to ≥ 1000 μmol m^{-2} s^{-1} (Teskey et al. 1984). Under full sun conditions, irradiance in both the clearcut and outside edge environments exceeded these limits, however, average irradiance in the inside edge environment was well below the light saturation point. Seedling growth in the inside edge environment was thus limited by light. We estimated that in the last 3 mo of the growing season the outside edge replicates received ~16% less light than the clearcut replicates due to afternoon shade created by the stand edge. Lower light may have limited net carbon gain by outside edge seedlings.

The optimal temperature for net photosynthesis of Pacific silver fir is 15 ± 1.5°C throughout the year, but net photosynthesis is usually within 10% of maximum between 10°C and 18°C (Teskey et al. 1984). Mid-summer high temperature compensation points are greater than 30°C (Teskey et al. 1984). The relatively low optimal temperature for net photosynthesis in Pacific silver fir, combined with temperatures among the three environments that varied by only a few degrees, indicates that temperature did not limit net photosynthesis in any of the environments.

Soil water deficits were minor, thus we did not consider moisture greatly limiting. The clearcut seedlings had the lowest water potentials on two occasions in late summer (Table 1), and stomatal limitations may have reduced photosynthesis on those days (Livingston and Black 1988). Although soil nutrients were not measured, we believe that higher daytime soil temperatures in the more exposed clearcut and outside edge environments led to greater rates of nitrogen mineralization (Lambers et al. 1998). In a site located 2 km from our study at a similar elevation, Prescott (1997) found *in-situ* rates of net nitrogen mineralization and concentrations of nitrate in forest floor and soil were greatest in a clearcut and least in the forest.

Differences in light availability among environments resulted in advance regeneration and planted trees converging in each environment with respect to physiology (foliar nitrogen concentration) (Figure 2) and relative growth rate. In low light, nutrient limited environments, plants generally have greater root:shoot ratios and decreased concentrations of soluble protein and Rubisco relative to plants in high light environments (Taiz and Zeiger 1998). Thus in the inside edge environment, advance regeneration, acclimated to low

light, maintained root:shoot ratios and foliar nitrogen concentrations while planted seedlings, acclimated to high light, allocated more biomass to roots and less nitrogen to leaves. In the clearcut, planted seedlings tended to stay the same while advance regeneration allocated more biomass to shoots and more nitrogen to leaves. As a result, relative growth rates converged in each environment for advance regeneration and planted trees.

Prior to release in 1989, we believe advance regeneration had high root:shoot ratios similar to the inside edge seedlings in 1993. Tucker et al. (1987) cite several studies of understory Pacific silver fir and grand fir (*Abies grandis*) trees with low root:shoot ratios. The combination of low nutrient availability and low irradiance on our study site, however, would lead to high initial root:shoot ratios. The high root:shoot ratio of inside edge seedlings was also because advance regeneration of Pacific silver fir grows horizontally as the lower stem is buried by organic matter. Guest (2001) excavated 70 advance seedlings of Pacific silver fir and found that seedlings < 50 cm tall had 10-70 cm of buried stem. The buried stems produce adventitious roots, therefore we included them in root biomass. Shoots of advance seedlings in the outside edge and clearcut environments were larger than inside edge seedlings, which reduced the proportional contribution of the buried stem to root:shoot ratios. Acclimation of root:shoot ratio was not observed in planted seedlings, because one growing season was not long enough to change biomass allocation significantly. In a nursery study, no differences were found among root:shoot ratios of 1-yr-old Pacific silver fir PSB 313B container seedlings grown for a second year in high and low light environments (Mitchell and Arnott 1995).

Four growing seasons after harvest, significant differences in leaf morphology were observed in advance regeneration among the three environments, with high SLA in the inside edge. Tucker et al. (1987) suggest that it may take 7 yr for Pacific silver fir to acclimate to overstory removal, therefore advance seedlings had acclimated fully by the end of our study. In seedlings planted in 1993, foliage expanded in the year of planting acclimated rapidly to differences in light among the three environments. Leverenz and Jarvis (1980) found that Sitka spruce (*Picea sitchensis*) could change foliar morphology in the first year if the tree was exposed to the new light conditions just prior to bud burst.

In the first growing season after planting, foliar nitrogen concentrations in planted seedlings in all environments declined from their pre-planting condition. In 1993, nitrogen concentrations in planted seedlings were highest in the inside edge environment (Figure 2) because shoot expansion was limited. Low nitrogen concentrations in planted seedlings in the high light environments was supported by their chlorotic appearance, but chlorosis may have been due to photooxidation. Foliage of newly planted seedlings may suffer damage from ultra-violet light at high elevation (Tucker et al. 1987). In the second growing season, foliar nitrogen concentrations of planted seedlings in the clearcut increased, but those in the outside and inside edge did not increase (Figure 2). We surmise that seedlings planted in the clearcut experienced rapid root growth, allowing increased nitrogen uptake. Shoot growth may not have increased proportionally, allowing accumulation of nitrogen. Five years after planting, foliar nitrogen concentrations were greatest in seedlings in the outside edge, and lower in clearcut and inside edge seedlings (Figure 2). Although foliar nitrogen concentration was low in clearcut seedlings, leaf weight and shoot size were greater in these plants (Figure 1), thus total nitrogen content was greater.

Three and four growing seasons after overstory removal, advance seedlings in the clearcut and outside edge environments had higher foliar nitrogen concentrations than inside edge seedlings (Figure 2). Greater foliar nitrogen in warmer environments is explained by the expected increased rates of nitrogen mineralization. By 1998, patterns of foliar nitrogen concentration in advance seedlings in the three environments were similar to planted seedlings, and foliar nitrogen in the higher light environments had declined due to growth dilution.

By 1998, foliar nitrogen concentrations were not significantly different between planted and advance seedlings, but were significantly below the 1.15% critical nitrogen concentration defined by Powers (1983) in all environments. In the clearcut and inside edge environments, foliar nitrogen concentrations were also below the average of 0.93% nitrogen for 26 to 37-yr-old trees sampled in 19 stands in western Washington

(Radwan et al. 1989). Although Radwan et al. (1989) suggest that Pacific silver fir may have a high nitrogen utilization efficiency, the low foliar nitrogen concentrations measured on our sites likely limited growth, supporting the contention that growth check observed in natural and planted Pacific silver fir saplings growing in montane clearcuts is associated with nitrogen deficiency (Husted 1982, Arnott and Beese 1995).

Despite apparent nitrogen limitation, growth rates of both planted and advance seedlings were greatest in the clearcut, followed by outside and then inside edge environments. RGR of the two regeneration types were not significantly different, and the pairs of height growth curves for each environment diverged only slightly (Figure 1). Although height of planted seedlings was greater than advance seedlings in all environments, this effect was due to differences in initial size. Other studies examining the response of naturally regenerated Pacific silver fir seedlings and saplings to irradiance or exposure by overstory removal demonstrate that both establishment (Gray and Spies 1996, 1997) and growth (Tucker et al. 1987, Klinka et al. 1992, Gray and Spies 1996) are greater with increased light. While Pacific silver fir is shade tolerant (Teskey et al. 1984, Mitchell and Arnott 1995) and survives suppressed in the understory for long periods of time (Klinka et al. 1992), when released by overstory removal Pacific silver fir increases height increment by the third growing season (Herring and Etheridge 1976, Tucker et al. 1987).

The effect of a clearcut on the edge environment of a forest has been documented (Chen and Franklin 1992), and we have confirmed that the edge effect of a forest also extends into the cut block. With increasing use of silvicultural systems that create more edge, the proportion of tree seedlings influenced by forest edge will increase. In this study, the growth of Pacific silver fir seedlings 12-17 m from the edge was reduced relative to those 60-65 m from the forest edge. Growth was reduced in both advance regeneration and planted trees. Growth limitations were, in part, due to reduced light, and possibly to reduced nitrogen availability. Shade-induced growth limitations would increase under nutrient stress. Further study is required to document the depth of edge influence for a wider variety of sites and edge aspects.

Acknowledgements

The authors gratefully acknowledge MacMillan Bloedel Ltd., Menzies Bay Division for their cooperation in locating a suitable study site; P. Puttonen for his help and advice in establishing this study; P. Price, A. Gammel and A. Harris for technical assistance; and J. Moran for reviewing an early draft of the manuscript. Funding for the project was provided by Forest Renewal BC.

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Received 14 June 2001
Accepted for publication 30 January 2002

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Patrick J. Brown and **David A. Dalton,**[1] Biology Department, Reed College, Portland, Oregon 97202-8199

In situ Physiological Monitoring of *Lobaria oregana* Transplants in an Old-growth Forest Canopy

Abstract

Lobaria oregana (lettuce lung lichen) is an abundant nitrogen-fixing cyanolichen in old-growth Douglas-fir forests of the Pacific Northwest. In this study, we used the Wind River Canopy Crane Research Facility to study nitrogenase activity, photosynthesis, and growth to clarify the potential for *Lobaria* to contribute fixed nitrogen to these forests and to better understand the ecological factors that determine the distribution of *Lobaria*. Pendants of *Lobaria* were placed at three positions in the canopy: top (62 m above the ground), middle (39 m), and bottom (2 m). There was a complex pattern of seasonal and spatial variation. Greatest growth was found at the middle position where there was a 19.3% increase in dry weight over the 13-mo study period. Lichens at the bottom position died after transplanting. Nitrogenase activity was consistently higher in the middle position and averaged 115 nmol C_2H_4 g^{-1} hr^{-1} for wet season measurements (February, March, and November) with a range of 0-310 nmol C_2H_4 g^{-1} hr^{-1}. Photosynthesis activity averaged 0.322 mg CO_2 g^{-1} hr^{-1} for the wet season with a range of 0-0.801 mg CO_2 g^{-1} hr^{-1}. Activities were strongly correlated with hydration except that hydration >200% inhibited photosynthesis. Laboratory experiments showed that photosynthesis increased at photosynthetic photon flux densities of up to 1000 µmol m^{-2} s^{-1}. This study supports the conclusion that *Lobaria* is a source of nitrogen input for these forests and addresses how the physiological activities of *Lobaria* respond both spatially and temporally to the extremely variable environment within the canopy.

Introduction

Lobaria oregana (lettuce lung lichen) is an epiphytic cyanolichen endemic to the old-growth forests of the Pacific Northwest. As a tripartite cyanolichen, it represents a three-way symbiosis between an ascomycete, a green alga *(Myrmecia),* and a cyanobacterium (*Nostoc*). While the alga acts as the primary photobiont, supplying the lichen with photosynthetic sugars, *Nostoc* acts to supply nitrogen that it fixes within specialized structures called cephalodia (Nash 1996).

This lichen has received recent attention both for its specificity to old-growth forests and for its ability to provide a significant source of nitrogen to this ecosystem. While *Lobaria* is essentially absent from stands < 80 yr old, it is abundant in old-growth stands where its distribution is heterogeneous but may exceed 1 metric ton ha^{-1} (McCune 1993). On three 400-yr old trees surveyed by McCune (1993)—one individual each of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*)—total cyanolichen biomass was 1.1, 22.9, and 2.3 kg. Sillett (1995) measured the biomass of 65 epiphytic lichen species, including *Lobaria oregana* and 14 other cyanolichens. Litterfall biomass of *L. oregana* was twenty times greater than the next most abundant cyanolichen, *Lobaria pulmonaria* (lungwort). In a survey by Pike et al. (1977), *L. oregana* represented more than half the total epiphyte biomass. *Lobaria* is absent from young stands

Denison (1979) estimated that *Lobaria* contributes 3-4 kg N ha^{-1} yr^{-1} to old-growth forests. Since cyanolichen abundance is so variable from site to site, however, it is hard to quantify the abundance and nitrogen contribution of *Lobaria* in a typical old-growth forest. Another complicating factor is that no further field measurements of nitrogenase activity in *L. oregana* have been reported since the Denison (1979) study.

The key nutritional role that cyanolichens such as *Lobaria* play in forest ecosystems has inspired several recent studies to define what constitutes suitable cyanolichen habitat. Transplant experiments using weight gain as an indicator of growth have led to mixed results. Sillett (1994) found that *Lobaria* transplants grew less on the forest edge than in the forest interior. Other transplant experiments showed no differences in growth between *Lobaria* transplanted to 35, 100, and 400-yr-old forests (Sillett and McCune 1998). McCune et al. (1997) determined that cyanolichens are concentrated in the light transition zone 13-37 m

[1] Author to whom correspondence should be addressed: E-mail: david.dalton@reed.edu

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above the forest floor, where light transmittance declines abruptly from 75% to 25% of the total light striking the top of the canopy.

We used *in situ* physiological measurements of *Lobaria* in the forest canopy to assess the contribution to the nitrogen nutrition of Pacific Northwest old-growth forests. These studies are of interest because previous work with *Lobaria* has been limited to use of loose thalli under artificial conditions and thus the significance of this species in the nitrogen budget of these forests remains unresolved. *In situ* measurements under natural light and temperature conditions have now become feasible due to the availability of the canopy crane. Such studies can provide insight into the environmental constraints that determine the distribution of *Lobaria* within the canopy as well as its absence from young stands. The specific objectives were: 1) to measure growth at different canopy positions during wet and dry seasons; 2) to measure net photosynthesis and nitrogenase activity at different hydration states, seasons, and canopy positions; and 3) to define photosynthetic light responses in controlled laboratory studies.

Methods

Study Area

This study took place at the Wind River Canopy Crane Research Facility (WRCCRF) in the Wind River Experimental Forest (Trout Creek Division) in the southern Washington Cascades (45° 49' N, 121° 55' W). WRCCRF maintains a Liebherr 550 HC construction crane that sits amid 12 ha of old-growth forest. With a height of 87 m and a horizontal reach of 85 m, the crane provides access to over 10^5 cubic meters of old-growth canopy for research purposes. The crane is operated jointly by the USDA Forest Service and the University of Washington.

Douglas-fir and western hemlock are co-dominant at the WRCCRF site. Other common canopy trees include western redcedar, Pacific silver fir (*Abies amabilis*), grand fir (*A. grandis*) and noble fir (*A. procera*). In the understory, the presence of snags, fallen logs, and the slow-growing Pacific yew *(Taxus brevifolia)* help characterize the site as old-growth. Over 114 species of lichens have been found in the 12-ha crane plot (McCune 1997). Average annual precipitation is approximately 250 cm, of which < 10% occurs between June and September. The average annual temperature is 8.7°C. Although elevation is <400 m, winter snowfall is typically heavy from December through February with an annual average of 233 cm. Monthly averages for temperature and precipitation for the nearby Carson fish hatchery are available online (Desert Research Institute 2001). Microclimatic data at the crane site for the days on which physiological measurements were made are presented in Table 1. A thorough description of the study site, including an annotated species list is available online (University of Washington 2001a).

TABLE 1. Meteorological data at 1200 hours from the WWCCRF on the dates when physiological measurements were made. Source: University of Washington (2001b).

Date	Height (m)	Temp. (°C)	Relative humidity (%)	Precipitation[1] (mm)	PAR[2] (W m^{-2})
23 Feb	2	2.73	100	14.3	-
	70	-	-	-	-
	2-open[3]	3.9	100	-	153
16 Mar	2	3.59	100	1.9	10.4
	70	4.49	61.9	-	-
	2-open	6.29	65.0	-	1154
7 Apr	2	4.09	93.3	1.2	9.9
	70	4.75	58.4	-	-
	2-open	5.82	58.0	-	1137
30 Sept	10	18.8	49.4	0	1167
16 Nov	2	10.3	100	1.0	8.9
	70	10.5	92.3	-	-
	2-open	11.2	98.7	-	130

[1]preceding 24 hr

[2]photosynthetically active radiation

[3]at 2 m height in an adjacent open field

Pendant Construction

Desiccated *Lobaria* litterfall was collected near the crane site on 17 October, 1998. The litterfall was cleaned of debris, cut into thallus pieces roughly 5 cm in diameter, and air dried for 48 hr. Older, interior portions of thallus without growing edges were not used. Thallus pieces were weighed individually and strung onto nylon fishing line (25-lb test) alternately with numbered beads to form pendants of 20 thallus pieces each (Denison 1988). Each numbered bead identified

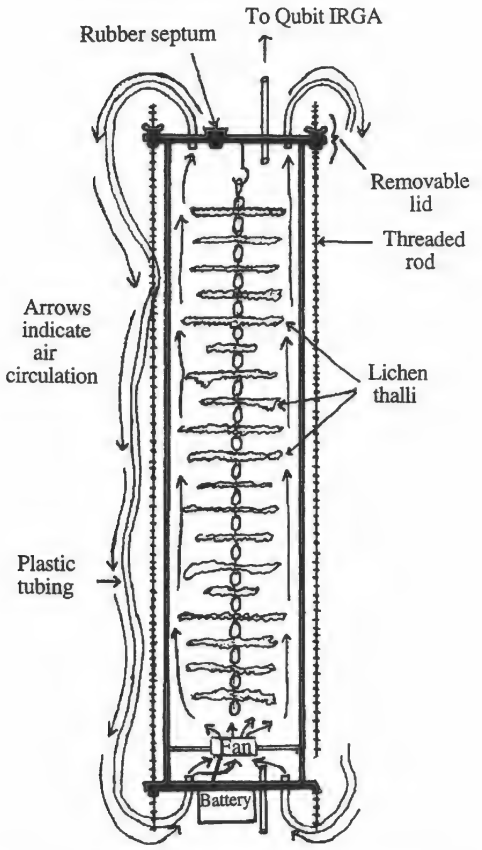

Figure 1. Plexiglas chamber used for physiological measurements of pendants of *Lobaria*. Twenty thallus fragments (~ 5 cm in diameter) were strung onto nylon fishing line and suspended in the chamber.

a specific thallus piece, so that the weight of lost pieces could be accounted for. Total pendant dry weights ranged from 15-17 g.

Five air-tight Plexiglas cylinders were constructed to accommodate the lichen pendants (Figure 1) during physiological measurements. Cylinders featured battery-powered fans (Radio Shack 12V DC Brushless) to maintain air circulation around each pendant during closed incubations. Tygon tubing connected each end of a cylinder to the system for measuring CO_2 exchange as described below. Rubber septa allowed gas injection and removal for the acetylene reduction assay. The total volume of each cylinder was 1.15 L.

Transplant Sites

Twenty pendants were constructed for transplantation to four different sites. Five pendants each were transplanted to three different sites in the old-growth canopy: top (62 m above the forest floor), middle (37 m), and bottom (2 m). Top and middle groups were both transplanted using the canopy crane to a single large Douglas-fir with a broken top. Pendants were hung from accessible branches using plastic cable ties. The top group was above the natural vertical distribution limit of *Lobaria*. Lichen genera common to this microhabitat include the alectoreoids (*Alectoria* and *Usnea* spp.), bone lichens (*Hypogymnia* spp.), and rag lichens (*Plastismatia* spp.). The middle group lay within the vertical distribution of many cyanolichens including *Lobaria oregana*, *Lobaria pulmonaria*, and *Pseudocyphellaria* spp. The bottom group was accessible from the ground, and pendants were hung from the lower branches of understory hemlock, yew, and vine maple (*Acer circinatum*) in a microhabitat dominated by bryophytes. *Lobaria* was present here only in the form of litterfall.

The remaining five pendants were transplanted to the understory (2 m) of an even-aged, single-species stand of ~45-yr-old Douglas-fir. This site was located about 8 km north of the WRCCRF site. Lichen diversity in this second-growth is greatly reduced compared to the old-growth site and arboreal cyanolichens are absent. No physiological measurements were taken from this group, but the pendants were retrieved in April 1999 to assess growth.

Measurements of CO_2 Exchange and Nitrogenase Activity

Pendants were transplanted in October 1998. Physiological measurements were taken in February, March, April, September, and November 1999. Measurements were always taken from the top group to the bottom group. Each pendant was removed from the tree, weighed, enclosed within a gas tight cylinder (Figure 1), and then measured for CO_2 exchange. This was followed within 15 min by the nitrogenase activity (acetylene reduction) assay. Cylinders were hung from the edge of the crane gondola to mimic natural light and temperature. Air for the CO_2 exchange assay was pumped up through tygon tubing that dangled several meters below the gondola. This

ensured that the air source was relatively free of human influence, yet representative of the humidity and temperature of each microclimate. After the assays were complete, the pendants were reattached to the tree. A typical measurement session on an individual pendant lasted 30 min.

A CO_2 analysis package from Qubit Systems, Inc. was used for all CO_2 exchange measurements. An infra-red gas analyzer (IRGA) for measuring CO_2 concentration was coupled with light, temperature, or humidity sensors through a serial box interface (SBI) capable of recording two inputs simultaneously. The SBI was connected to a Macintosh Powerbook 3400c equipped with Qubit datalogging software. The IRGA was calibrated using standards containing 0 and 500 ppm CO_2. Net photosynthesis was measured for each pendant as the difference between ambient [CO_2] and the [CO_2] of a pendant-containing cylinder. Typical values for $\Delta[CO_2]$ were 50-100 ppm. Air was pumped through the pendants at a flow rate of ~21 L hr^{-1}. At this rate a stable experimental reading was obtained in ~5 min.

The CO_2 exchange rates of individual *Lobaria* fragments were also tested in the laboratory. A Qubit Plexiglas cuvette (1 x 3 x 3 cm) and a flow rate of 2.7 L hr^{-1} were used for these laboratory experiments. Photosynthetic photon flux density (PPFD) was determined with a portable LI-COR model LI 185B quantum meter.

The acetylene reduction assay was used to measure nitrogenase activity. Acetylene was generated by reacting calcium carbide with water. Sufficient acetylene was injected into the cylinder to achieve a concentration of 10% by volume. The cylinder was shaken vigorously, vented to atmospheric pressure, and the battery-powered fan was engaged. A 1-mL gas sample was then withdrawn by syringe for a time zero reading. After 20 min of incubation, three more 1-mL gas samples were taken. Syringes were inserted into rubber stoppers to prevent leakage during transport back to the laboratory where the ethylene content of each sample was determined with a Varian model 330 gas chromatograph equipped with a 0.318 x 76 cm stainless steel column of Poropak N and a flame ionization detector. The initial gas sample (at t=0) was subtracted from the mean of the three subsequent gas samples (at t=20) for each cylinder to control for the slight (but not negligible) background levels of ethylene that are normally present in acetylene. An additional control consisting of a chamber with 10% acetylene but lichens showed no change in background levels of ethylene during a typical 20-min assay period.

Thallus Weight and Hydration

The initial dry weight of each pendant was measured in October 1998. In April 1999, all pendants were removed from the site, air-dried for 48 hr, re-weighed, and returned to the canopy. In November 1999, all pendants were removed and weighed again after 48 hr of air-drying. This allowed us to measure growth during the wet season (October-April) and dry season (April-November) separately.

The wet weight of each pendant was determined prior to each physiological measurement session. The ~10.5 g weight of the non-absorbent pendant components (beads, fishing line, and a trace of silicone sealant) was subtracted from the total pendant weight to determine the weight of the hydrated lichens, which was then used to calculate hydration as follows:

$$\text{Hydration (\%)} = ((\text{wet wt.}-\text{dry wt.})\ (\text{dry wt})^{-1}\ ) * 100.$$

Missing thallus pieces were noted so that their dry weights could be deducted from the total pendant dry weight.

Oven-dried weights and not air-dried weights are typically used to calculate thallus weight and hydration. However, oven-dried thalli cannot be used for further physiological study. Therefore, sacrificed thalli (Sillett 1994) were weighed after 48 hr of air-drying and again after a further 24 hr of oven-drying at 70°C. Oven-dried thalli weighed ~ 10% less than thalli collected and air-dried in both October and April. This ratio was used to determine theoretical oven-dried weights of pendants for calculations of thallus hydration, so that a hydration level of 100% represents 1 g of water for each 1 g of oven-dried thallus. These calculations were based on the assumption that no dry weight gain had occurred since the last determination of oven-dried weight.

Differences Between Laboratory and Field Measurements

The laboratory measurements of CO_2 exchange and nitrogenase activity differed from field measurements in several ways. First, quantities of lichen for each lab sample were 0.1-0.6 g compared

to 4.5-6.5 g for each field sample. In the laboratory, CO_2 exchange was measured in a 9 cm^3 Qubit cuvette and nitrogenase activity in 15-mL test tubes, whereas cylinders used for both field measurements were 1150 cm^3. Flow rates through the Qubit cuvette were correspondingly lower (2.7 L hr^{-1} versus 21 L hr^{-1} for the field chambers). House compressed air provided a source of CO_2 with a stable concentration for the laboratory experiments. Dry air from the lab outlet was passed through a solution of saturated NaCl to create high humidity levels that were favorable for lichen activity.

Results

Growth of Transplants

Pendants transplanted to the top and middle positions of the old-growth canopy gained weight during the experiment whereas those at the bottom position in the old-growth site lost weight (Figure 2). During the wet season (October to April), both top and middle groups registered nearly identical weight gains (16.2% and 16.4%). During the dry season (April to November), however, the top group suffered a mean weight loss (-4.1%) while the weight gain of the middle group was much reduced but still positive (2.9%). Therefore, the overall weight gain (October to November) of the middle group was greater (19.3% vs. 12.0%).

Transplants to the forest understory (2 m) of both old-growth (bottom) and second-growth (bottom-45 yr) gained significantly less weight than their counterparts in the canopy ($P<0.005$, Figure 2). The old-growth bottom group became discolored soon after transplanting, lost weight (6.1% for the wet season) and developed an unpleasant fishy odor. The second-growth bottom group appeared healthy in April 1999, showed some growth (4.8% for the wet season), but had been heavily grazed. The low weight gain for the second-growth bottom group probably reflects a higher incidence of grazing rather than the lack of suitability of this microclimate for *Lobaria* growth. Both bottom groups were removed from the field in April 1999.

Hydration Effects on Physiological Activity

Some of the variation in physiological activity of *Lobaria* can be explained by hydration alone without regard to other factors such as season, temperature, or light. In general, both net photosynthesis (NP) and nitrogenase activity (acetylene reduction) increased markedly with increases in hydration (Figure 3A-E). In the case of NP, hydration levels >200% were less favorable than lower levels (Figure 3B). This decline at high hydration levels was not observed for nitrogenase activity (Figure 3E).

Seasonal Variation in Physiological Activity

Hydration status, photosynthesis, and nitrogenase activity were measured during five canopy crane visits made over 10 mo from February through November 1999 (Figure 4). This sampling frequency

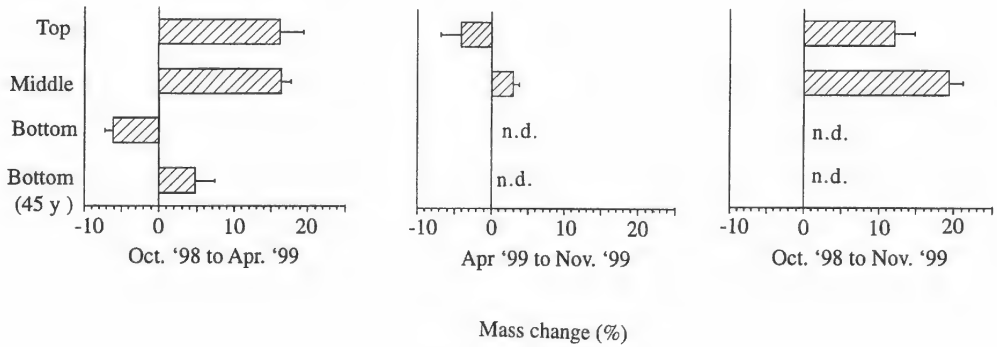

Figure 2. Seasonal weight gains in *Lobaria* pendants which were transplanted to either Top (A, 62 m above the ground) or Middle (B, 39 m above the ground), positions in the old-growth canopy at the Wind River Canopy Crane Research Facility or to the bottom (2 m) position of a 45-yr-old stand of Douglas-fir. Each bar represents the mean of 5 replicates ± 1 SE.

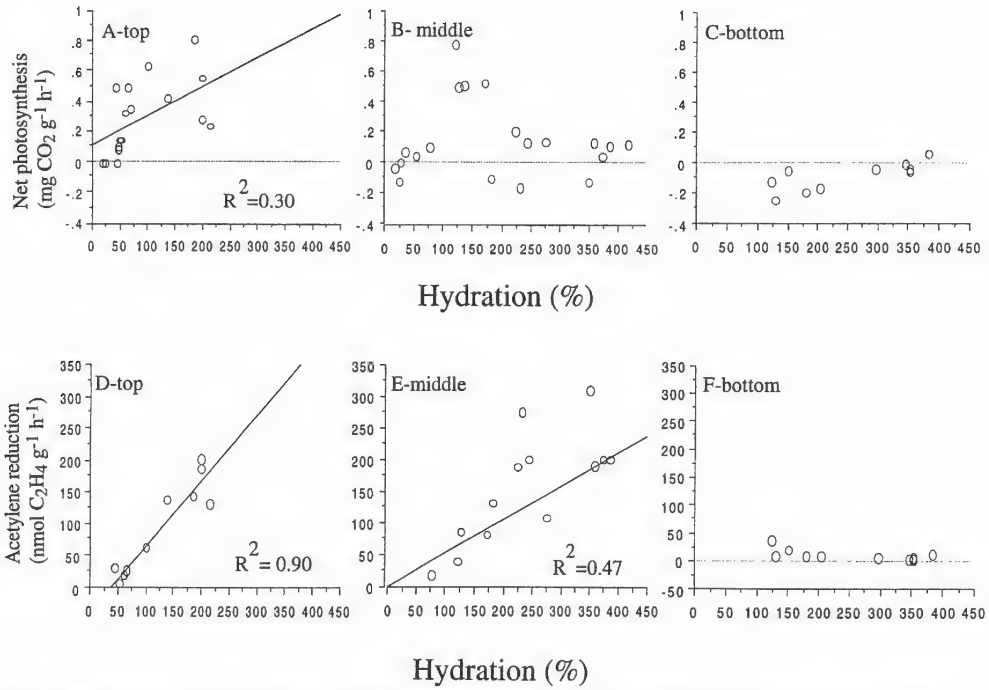

Figure 3. Effects of hydration on rates of photosynthesis (A) and nitrogenase activity (B) by pendants of *Lobaria* transplanted to the top (A, D), middle (B, E) or bottom (C, F) position of an old-growth canopy. Measurements were made between February and November 1999.

provides valuable snapshots of physiological conditions, but can not capture the full effects of daily or monthly variation in weather. The group in the canopy middle (39 m) remained consistently more hydrated than the group in the canopy top (62 m) throughout the wet season (Figure 4A, P=0.0007). During the dry season, hydration was uniformly low for both groups, but declined from April (44.9%) to September (22.2%). The hydration values in the old-growth bottom group were similar to those of the middle group in February and March. When considered along with the severe dark coloration and odor of decay, it was apparent that the lichens at this position were necrotic and consequently no further measurements were taken at this position.

The responses of net photosynthesis (NP) were complicated by the decreases observed at hydration levels >200%. Consequently, the middle position was sometimes too wet for optimal photosynthesis (e.g., February, Figure 4B), whereas such high hydration levels were not observed at the top position. Photosynthetic rates for top-February, top-November, and mid-March were roughly comparable with values near 0.5 mg CO_2 g^{-1} hr^{-1}. Net carbon loss occurred both in situations of high hydration (September) and low hydration (November) in the middle canopy. Pendants at the old-growth bottom position showed net loss of CO_2 for both February and March.

Nitrogenase activity was detected only during the wet season (Figure 4C). Nitrogenase activity was consistently higher in the middle group, likely as a consequence of the shading and higher moisture content in this microclimate. The maximum rate observed was 222 ± 32 nmol C_2H_4 g^{-1} hr^{-1} (March, middle, n = 5). The lichens in the top group were more exposed to wind and direct sunlight that resulted in rapid desiccation and thus lower activity of nitrogenase. Pendants at the bottom

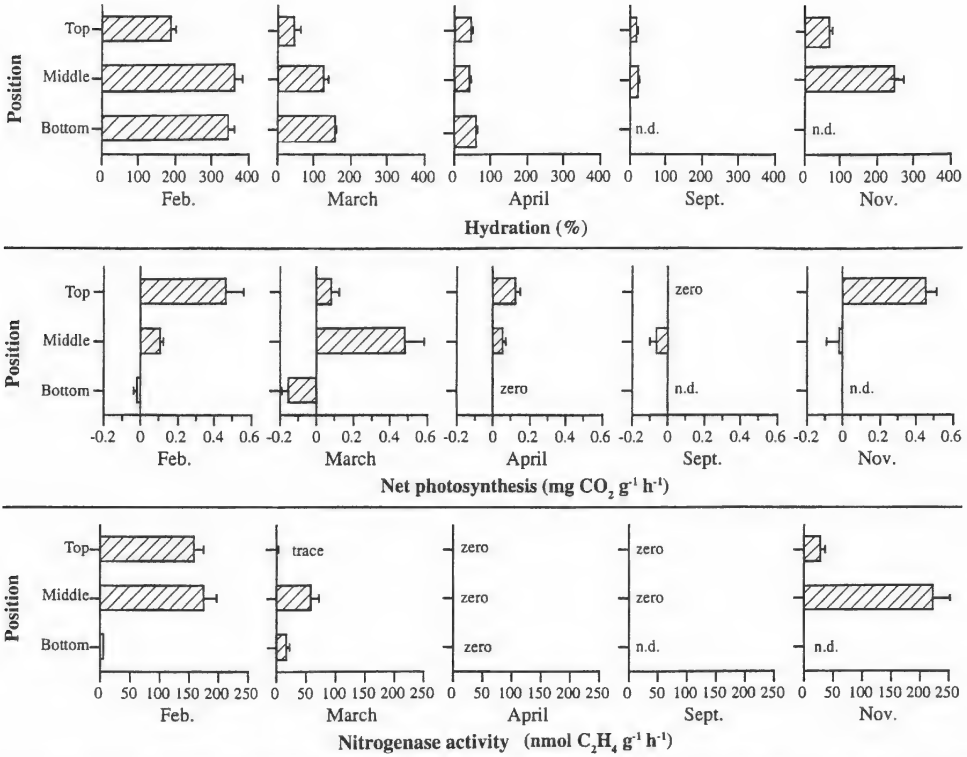

Figure 4. Seasonal variation in hydration, rates of photosynthesis, and nitrogenase activity in pendants of *Lobaria* which had been transplanted to various positions (top, middle, or bottom) in an old-growth canopy. Each bar represents the mean of 5 replicates ± 1 SE.

position showed very low activity in February and March.

CO_2 and Light Limitations of Photosynthesis

Laboratory studies at ambient [CO_2] (350 ppm) indicated that NP in *Lobaria* followed a light saturation curve that reached 50% of maximum at only 100 µmol m^{-2} s^{-1}. Near saturation was reached around 400 µmol m^{-2} s^{-1} and further increases in PPFD up to 800 µmol m^{-2} s^{-1} resulted in only a slight increase in NP. Thallus pieces at different hydration levels or concentrations of CO_2 showed different maximum rates but followed the same pattern of light saturation. Higher concentrations of CO_2 led to elevated rates of NP at all light levels tested (Figure 5). Even in the absence of light, net CO_2 loss was lower at high [CO_2]. Thalli failed to achieve net carbon gain, even if light saturated, at a [CO_2] of 250 ppm.

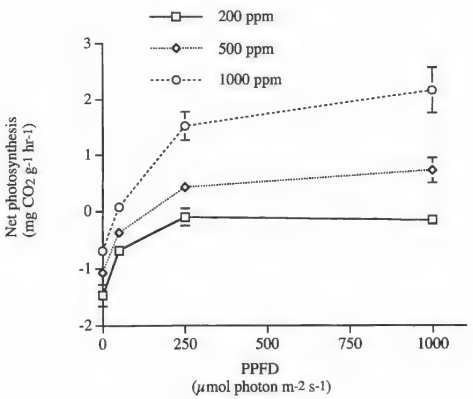

Figure 5. Effects of increasing PPFD on photosynthesis in *Lobaria* pendants. Measurements were at room temperature under controlled laboratory conditions with different concentrations of CO_2 as indicated. Each data point is the mean of 5 replicates ± 1 SE.

Limiting Factors to Nitrogenase Activity

The effects of drying and re-wetting were examined with *Lobaria* samples that were harvested directly from branch surfaces using the canopy crane and returned to the laboratory. Fresh epiphytic material was used because lichens from litterfall had highly variable and unreliable rates of nitrogenase activity. Thalli that had been dried and then rewetted showed considerably less nitrogenase activity (mean of 145 nmol C_2H_4 g^{-1} hr^{-1}) than those that were assayed immediately (mean of 477 nmol, C_2H_4 g^{-1} hr^{-1}, n = 12 , P <0.0001). Rates of nitrogenase activity in the laboratory (18-887 nmol C_2H_4 g^{-1} hr^{-1}) were much higher than those obtained at similar hydration levels in the field (Figure 4C). This discrepancy, which was probably due to differences in light, temperature, humidity, and specific assay conditions, demonstrates the importance of making physiological measurements under natural conditions and as unobtrusively as possible. Although *in situ* field measurements may be under sub-optimal conditions, they are a more realistic indication of the true role of *Lobaria* in these forests.

Discussion

Growth

Mean annual weight gains of 12.0% (top) and 19.3% (middle) are comparable to other reported annual growth rates for transplanted *Lobaria*. Denison (1988) reported growth rates of 43-67% over 3 yr, or 14-22% per yr. McCune et al. (1996), using loops rather than pendants, found an annual growth rate of 4-11%. Sillett (1994) performed reciprocal transplants on *Lobaria* from tree crowns in the forest interior and the forest edge and found annual growth of 6-14%. A further study by Sillett and McCune (1998) reported annual growth between 15-18% for forests of three age classes from 35 to 700 yr old.

Photosynthesis and Nitrogenase Activity

The hydration response observed for net photosynthesis (Figure 3A-C) closely supports the optimal range of 75-175% reported by Sundberg et al. (1997) for *L. pulmonaria.* The values for nitrogenase activity shown here (Figure 3D-F) are close to those reported by Denison (1979), the only other study to investigate nitrogenase activity by *Lobaria* in the field. Denison reports an average nitrogenase activity of 160 nmol C_2H_4 g^{-1} hr^{-1} for two winter wet seasons (September-June), with rates ranging from 0-845 nmol C_2H_4 g^{-1} hr^{-1}. In comparison, canopy transplants in this study averaged 115 nmol C_2H_4 g^{-1} hr^{-1} for wet season measurements (February, March, and November), with a range of 0-310 nmol C_2H_4 g^{-1} hr^{-1}. The correlation between nitrogenase activity and hydration (R^2= 0.81 if the bottom group is excluded) is remarkable, considering that measurements were taken across a wide range of light and temperature regimes.

The rate of photosynthesis averaged 0.322 mg CO_2 g^{-1} hr^{-1} for the wet season (top and middle positions combined) with a range of 0-0.801 mg mg CO_2 g^{-1} hr^{-1}. There are no values in the literature for rates of photosynthesis by *L. oregana*; however, our values closely match the data reported for *L. pulmonaria* by Sundberg et al. (1997) who reported a maximum rate of 2.18 µmol CO_2 m^{-2} s^{-1} which we calculate to be equivalent to 0.81 mg CO_2 g^{-1} hr^{-1}.

There is a narrow range of conditions in which NP and nitrogenase activity are both carried out at appreciable rates (Figure 4B-C, top-February). In November, NP and nitrogenase activity were almost mutually exclusive. These results underscore that lichen health cannot be maintained under static conditions, since no single condition is optimal for all physiological functions.

While both light and [CO_2] potentially limit the growth of *Lobaria* in its natural habitat, high light levels provide no obvious benefit and may be harmful (Gauslaa and Solhaug 1999). Based on the laboratory results shown here (Figure 5), *Lobaria* is able to take advantage of supraambient [CO_2] such as might result from transitory CO_2 fluxes. The magnitude and occurrence of such [CO_2] fluxes in forest canopies is the subject of current research at WRCCRF.

In lichens, the ability to fix N_2 recovers more slowly following desiccation than does NP (Kershaw 1985). The data shown here do not establish how long after rewetting this effect lasts in *Lobaria.* However, future field measurements of nitrogenase activity in lichens should address not only factors such as hydration and temperature, but also the time since the last dehydration event.

Lobaria contributes to the nitrogen budget of temperate rain forests of the Pacific Northwest. Nutrient cycling in these forests is generally efficient with little loss of nutrients from the system, however, precise nitrogen budgets are difficult to construct. This conservation of nutrients, along with the great age and stability of these forest communities, means that even the modest amounts of N_2 fixed annually by *Lobaria* can account for a substantial proportion of newly accrued, available nitrogen. We estimate the rate of nitrogen accretion to be approximately 2 kg N ha^{-1} yr^{-1} based on our observed value for the annual growth rate (19.3 %, middle position), the concentration of nitrogen in *Lobaria* thalli (2.1%, Denison 1979), and the typical biomass of cyanolichens in these forests (546 kg/ha) (Sillett and McCune 1998). We did not attempt to estimate nitrogen accretion on the basis of our acetylene reduction data because the conversion factor of acetylene reduced to N_2 fixed often varies substantially from the theoretical values of 3:1 or 4:1. However, our estimates of nitrogen accretion based on growth and biomass are similar to previous estimates (Denison 1979) in which a ratio of 3:1 was assumed.

Other potential sources of nitrogen are even more meager since other N_2-fixing symbioses (e.g. legumes, alder) are not common in these old-growth forests . The leafy liverwort *Porella*, which is abundant in these forests and forms a N_2-fixing symbiosis with *Nostoc* (Dalton and Chatfield 1985), may contribute to nitrogen accretion, but this issue has not been examined. Furthermore, precipitation in the Pacific Northwest contains little dissolved fixed nitrogen. We estimate nitrogen input from precipitation to be only about 0.6 kg N ha^{-1} yr^{-1} based on the annual precipitation total for this site and the nitrogen content of 1.8 μmol N L^{-1} in precipitation in western Washington (Edmonds et al., 1991). Finally, we note that Edmonds et al. (1991) also observed that the [NH_4^+] of stem flow was nearly sevenfold higher than the initial concentration in precipitation. They attributed this increase to leaching of nitrogen fixed by *Lobaria*. If this interpretation is correct, than our estimate of the rate of nitrogen accretion based on weight changes may be a gross underestimate since leached nitrogen is not accounted for in this method. Our studies support earlier evidence for the importance of N_2 fixation by *Lobaria* in these forests and also illustrate strikingly the difficulties of accurately quantifying this process due to the complexity of seasonal and positional (within-canopy) variations.

Acknowledgements

This work was supported in part by an Undergraduate Biological Sciences Education Initiative grant from the Howard Hughes Medical Institute. Additional support and assistance was provided by the Wind River Canopy Crane Research Facility which is operated by the USDA Forest Service and the University of Washington.

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Received 3 March 2001
Accepted for publication 1 February 2002

Evelyn L. Bull,[1] USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850

and

David B. Marx, Department of Biometry, 103 Miller Hall, University of Nebraska, Lincoln, Nebraska 68583-0712

Influence of Fish and Habitat on Amphibian Communities in High Elevation Lakes in Northeastern Oregon

Abstract

Declines in lentic breeding amphibians in the western United States, particularly in relatively pristine areas, emphasize the need for information on the distribution, abundance, and ecology of these species. In 2000 and 2001, we surveyed 43 high elevation lakes in northeastern Oregon to determine the influence of introduced trout and of habitat characteristics on the reproduction of native amphibians occurring there. Long-toed salamanders and Pacific treefrogs were negatively affected by introduced trout. Habitat characteristics exerted more influence on the abundance of eggs and larvae of western toads and Columbia spotted frogs than the presence of trout. Our results indicate that the presence of fish may be detrimental to amphibian biodiversity in high elevation lakes.

Introduction

Recent increased awareness that amphibian populations have declined on a global scale (Houlahan et al. 2000) has increased the need for the understanding of amphibian communities. The rapidity and magnitude of declines of some species, particularly some lentic breeding amphibians in the western United States (Carey 1993, Sherman and Morton 1993, Corn 1994, Fisher and Shaffer 1996, Drost and Fellers 1996), emphasize the need for baseline data on distribution and abundance of amphibians. Some of the agents blamed for amphibian declines include increased ultraviolet radiation (Blaustein et al.1994a), pathogenic fungi (Blaustein et al. 1994b, Kiesecker and Blaustein 1997), habitat alteration, acid precipitation, toxicants, global climate change (Wyman 1990), bacterial pathogens (Bradford 1991), and introduction of non-native predators (Hayes and Jennings 1986, Fisher and Shaffer 1996, Knapp et al. 2001a).

An increasing amount of literature is available on the negative influence of fish predators on amphibians. Mountain yellow-legged frogs (*Rana muscosa*) appear to have been eliminated by introduced fishes in many locations in the Sierra Nevada, by direct predation on tadpoles (Knapp and Mathews 2000) and possibly by the isolation of remnant populations by fish in the intervening waters (Bradford et al. 1993). The decline of the Cascades frog (*R. cascadae*) has been linked to the presence of non-native predatory fish in California (Fellers and Drost 1993). Salamanders appear to be particularly vulnerable to fish predation (Semlitsch 1988, Corn et al. 1997, Tyler et al. 1998, Pilliod and Peterson 2001). In addition to the direct predation by fish on amphibian eggs (Grubb 1972), larvae, and adults (Cochran 1983), fish may be responsible for introducing pathogens to amphibian populations (Blaustein et al. 1994b). *Saprolegnia ferax*, a water mold that affects fish, was largely responsible for egg mortality in one population of toad eggs in Oregon (Blaustein et al. 1994b). The presence of fish may alter the foraging behavior of amphibians and influence growth and subsequent survival of both larvae and adults (Bradford 1983, Kiesecker and Blaustein 1998, Tyler et al. 1998).

Amphibian declines in high elevation lakes are of particular interest because these sites lack human-caused disturbances except for climatic effects, air-borne pollutants, and introduced fish. Only four species of native amphibians occur in lakes in the mountains of northeastern Oregon: long-toed salamander (*Ambystoma macrodactylum*), western toad (*Bufo boreas*), Pacific treefrog (*Pseudacris regilla*), and Columbia spotted frog (*Rana luteiventris*). Two of these species, the Columbia spotted frog and western toad, have

[1] Author to whom correspondence should be addressed. E-mail: ebull@fs.fed.us

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generated a disproportionate share of the concern about unexplained declines in other areas of the western United States (Blaustein et al.1994b, Corn 1994). Our objective was to determine the influence of introduced trout and of habitat characteristics on amphibian populations in high elevation lakes in northeastern Oregon.

Methods

Study Areas

For this study we selected 43 high elevation lakes in northeastern Oregon, 20 with fish and 23 without fish. We used lakes with and without fish in the same basin and within 8 km of a road. Lakes containing fish had been stocked in the past 10-50 yr with eastern brook trout (*Salvelinus frontinalis*), rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarki henshawi*), or kokanee (*O. nerka*). All lakes that were presumably capable of supporting fish populations contained them. Pilliod and Peterson (2001) suggested that lakes > 1 ha in surface area and > 4 m deep could support fish in high elevation lakes in Idaho. None of the lakes in our study had historic fish populations. Five of the lakes are currently being stocked, with rainbow trout only.

Twenty-four of the lakes were in the Elk Horn Mountains (Union, Baker, and Grant Counties), 13 in the Wallowa Mountains in the Natural Recreation Area (Wallowa County), and six in the Eagle Cap Wilderness Area (Wallowa County) in northeastern Oregon. Elevation of the lakes ranged from 1,800 to 2,972 m. Lake size ranged from 0.4 to 34.8 ha, although most (77%) were < 5 ha in size. All lakes were permanent with a maximum water depth of 0.5 to 15.6 m. All lakes had a silt substrate, except two that had a gravel and boulder substrate. The dominant emergent vegetation consisted of sedges (*Carex* spp.) at all lakes, except one that was dominated by cattails (*Typha latifolia*).

Amphibian Surveys

Each lake was surveyed three times during the summer in 2000 and 2001 using standard practices for surveying breeding sites to document abundance of long-toed salamanders, western toads, Pacific treefrogs, and Columbia spotted frogs (Scott and Woodward 1994). In each summer, the first visit occurred as soon after snow melt as access allowed to search for adults and egg masses (between May and July depending on elevation). The objective of this visit was to locate egg masses of western toads and Columbia spotted frogs; eggs of long-toed salamanders had been deposited before many of the lakes were accessible and hatching had begun. Additional egg masses were counted on a second visit 1-2 wk after the first. The third visit was timed to correspond with the presence of larval stages from mid-July to early August.

Actual counts of egg masses or strings of the western toad and Columbia spotted frog were recorded. An accurate count of treefrog and long-toed salamander eggs could not be obtained because of the cryptic nature of their eggs relative to the other two species. Consequently, egg abundance of treefrogs and salamanders was classified as absent, scarce (less than 10 masses), or abundant (more than 10 masses).

Relative abundance of larvae was determined by dip netting where concentrations of larvae occurred (Shaffer et al. 1994, Crisafulli 1997), which was usually in the littoral zone. Twelve sweeps were made along the shore at each lake with a rectangular net 33 cm wide with a mesh size of 2 mm. A sweep consisted of a 1-m sweep perpendicular to the shore following the bottom contours, which typically occurred in water < 25 cm deep. Twelve sweeps covered 4 m^2 of area, thus the total number of larvae in 12 sweeps was divided by 4 to determine the number of larvae per m^2. Salamander larvae < 50 mm in total length were classified as first-year, while those that were longer were considered second-year.

Habitat Quantification

We measured 12 habitat variables at each lake during the first visit to determine the importance of habitat in predicting presence and abundance or each amphibian species (Table 1). The presence and species of trout were determined from field observations, consultations with fisherman, and stocking records (Oregon Department of Fish and Wildlife, La Grande, Oregon, personal communication). Historic records of stocking seemed to portray current occurrence based on our observations and those of fisherman; only one shallow lake (< 4 m deep) had been stocked previously but showed no evidence of fish during this study.

TABLE 1. Habitat variables measured at 43 high elevation lakes in northeastern Oregon, 2000-2001.

Variable	Method of Measurement or Categories Used
Elevation at lake (m)	Measured on topographic maps
Size of lake (ha)	Obtained from Oregon Department of Fish and Wildlife records
Lake type	Year round outlet, temporary outlet, no outlet
Maximum lake depth (m)	Obtained from Oregon Department of Fish and Wildlife records
North shore with shallow water (<20 cm deep) and without emergent plants (m)	Measured with tape
South shore with shallow water (<20 cm deep) and without emergent plants (m)	Measured with tape
North shore with shallow water (<20 cm deep) and emergent plants (m)	Measured with tape
South shore with shallow water (<20 cm deep) and emergent plants (m)	Measured with tape
Distance to forest edge (m)	Measured with tape
Marshy area adjacent to lake (ha)	Measured with tape or estimated
Talus adjacent to lake (ha)	Measured with tape or estimated
Coarse woody debris (any wood > 1m in length and > 10 cm in diameter)	Rated as:0-none, 1-scarce (1-5 logs), 2-moderate (5-25 logs), and 3-extensive (>25 logs)
Degree of isolation	No. of permanent water bodies within 1 km determined from topographic maps
Dissolved oxygen (mg/l)	Measured in afternoon in July 2000 with portable YSI meter (Model 55)
pH	Measured in afternoon in July 2000 with portable meter

We recorded the following habitat characteristics at oviposition sites: water depth, distance from shore, presence or absence of emergent plants, distance between the shore and the edge of emergent plants, the percent of area within a 3-m radius covered by coarse woody debris in the water, and side of lake shore (north, south, east, west). Egg masses > 30 m apart were considered separate oviposition sites for Columbia spotted frogs and western toads. Characteristics were recorded only once at each lake for treefrogs and salamanders at the site with the highest density of eggs.

Analytical Methods

For the analysis, we used the maximum number of egg masses or strings and larvae observed in either of the 2 yr at each lake. Numbers of egg masses for Columbia spotted frogs and strings of western toads, and numbers of larvae of all species, were compared between lakes with and without fish using t tests. Categorical values of abundance of eggs for long-toed salamanders and Pacific treefrogs were compared between lakes with and without fish using Mantel-Haenszel chi-square analyses (Agresti 1990). The influence of independent habitat and fish variables on amphibian abundance was determined with regressions. All variables were first subjected to all possible regressions and the most important variables were noted to be used as a starting point for the nonnormal regressions. Count data were examined, and it was determined that the negative binomial distribution fit the data better than any other distribution. Using the negative binomial distribution, a backward stepwise regression was conducted and the best model chosen. For ordinal data, a stepwise logistic regression was used to determine the best model. In all cases, logical competing models were compared to the final model to insure that the chosen model was appropriate. The log of lake size and lake size were used, because the majority of lakes were < 5 ha with a few large lakes.

Results

Of the 43 lakes, 22 contained reproducing Columbia spotted frogs, 18 western toads, 32 treefrogs, and 27 long-toed salamanders. Lakes with fish contained an average of 1.8±0.3 species of amphibians, while fishless lakes averaged

TABLE 2. Number of amphibian taxa at 43 high elevation lakes with and without fish in northeastern Oregon, 2000-2001.

Number of Amphibian Taxa	Number of Lakes without Fish	Number of Lakes with Fish
0	2	4
1	0	6
2	6	1
3	9	8
4	7	1

2.7±0.2 species (Table 2). Thirteen lakes contained eastern brook trout only, six contained both eastern brook and rainbow trout, and one contained eastern brook trout, rainbow trout, cutthroat trout, and kokanee.

Long-toed Salamander

Abundance of egg masses and number of larvae of long-toed salamanders were significantly higher in lakes without than in lakes with fish ($\chi^2 = 20.07$, $P < 0.01$; $t = 2.14$, $P = 0.04$) (Table 3). Salamander eggs or larvae occurred in 20 of the 23 lakes without fish, in contrast to 7 of the 20 lakes with fish. In the majority of high elevation lakes, 2 yr are required for larvae to metamorphose (Leonard et al. 1993). No second-year larvae were found in lakes with fish, whereas they were found in 10 lakes without fish. Salamander eggs were attached to branches, plants, or on the lake substrate in deeper water and farther from the shore than the other amphibian species we observed (Table 4). Salamander egg mass abundance was best predicted by elevation and absence of brook trout using logistic regression, while larvae abundance was best predicted by absence of brook trout and presence of rainbow trout (Table 5).

Western Toads

Of the 18 lakes with western toad reproduction, 11 lacked fish. One to four oviposition sites with

TABLE 3. Mean (SE) numbers of eggs and larvae at lakes with and without fish of long-toed salamanders, western toads, Pacific treefrogs, and Columbia spotted frogs in high elevation lakes in northeastern Oregon, 2000-2001.

Characteristic	Salamander	Toad	Treefrog	Spotted frog
No. egg masses in lakes without fish	1.4[1]	2.6 (1.4)	1.6[1]	14.4 (6.4)
No. egg masses in lakes with fish	0.2[1]	4.0 (2.2)	0.7[1]	9.8 (5.3)
No. larvae/m^2 in lakes without fish	1.9 (0.6)	3.4 (2.6)	18.1 (10.6)	4.0 (2.1)
No. larvae/m^2 in lakes with fish	0.4 (0.2)	23.6 (14.7)	4.7 (2.7)	2.6 (1.0)
No. lakes with species	27	18	32	22

[1] These values are means of categorical data when 0 = no eggs, 1 = eggs were scarce, and 2 = eggs were abundant.

TABLE 4. Mean (SE) habitat measurements taken at oviposition sites of long-toed salamanders, western toads, Pacific treefrogs, and Columbia spotted frogs in high elevation lakes in northeastern Oregon, 2000-2001.

Characteristic	Salamander	Toad	Treefrog	Spotted frog
Water depth (cm)	29.1 (1.5)	8.4 (0.6)	11.1 (0.6)	10.6 (0.4)
Distance to shore (m)	142.2 (3.0)	83.6 (3.2)	144.7 (2.7)	117.5 (2.2)
Vegetation width (m)	4.4 (1.1)	5 (0.7)	23.4 (1.5)	23.7 (1.1)
Coarse woody debris (%)[1]	3.5 (0.8)	11.3 (0.9)	8.7 (0.8)	4.6 (0.5)
Shore (%)[2]				
North	60	53	50	32
South	20	27	20	29
East	10	13	15	21
West	10	7	15	18
No. lakes with species	27	18	32	22

[1] Percent of area within a 3-m radius of eggs that was covered by coarse woody debris in the water.

[2] Percent of oviposition sites that occurred on each aspect of the lake shore.

TABLE 5. Variables selected in a regression analysis that best explain the variability in abundance of eggs and larvae of long-toed salamanders, western toads, Pacific treefrogs, and Columbia spotted frogs at 43 high elevation lakes in northeastern Oregon, 2000-2001.

Species/life stage	Variables (coefficient, χ^2)
Long-toed salamander	
Eggs	Elevation (-0.007, 8.10, $P \leq 0.01$)
	Brook trout presence (-4.165, 17.68, $P \leq 0.01$)
Larvae	Brook trout presence (-4.575, 5.05, $P = 0.02$)
	Rainbow trout presence (4.078, 3.82, $P = 0.05$)
Western toad	
Eggs	Log of lake size (1.031, 8.56, $P \leq 0.01$)
	Water depth (-0.287, 3.99, $P = 0.05$)
	Coarse woody debris (1.043, 8.03, $P \leq 0.01$)
	North shore with shallow water and vegetation (-0.006, 2.83, $P = 0.09$)
	North shore with shallow water and no vegetation (0.005, 5.07, $P = 0.02$)
Larvae	Lake size (0.169, 1.80, $P = 0.18$)
	Coarse woody debris (1.821, 7.81, $P \leq 0.01$)
Pacific treefrog	
Eggs	Elevation (-0.008, 9.18, $P \leq 0.01$)
	Brook trout presence (-3.896, 16.12, $P \leq 0.01$)
	Rainbow trout presence (2.466, 5.54, $P = 0.02$)
Larvae	pH (-1.878, 7.19, $P \leq 0.01$)
	Log of lake size (0.523, 6.07, $P \leq 0.01$)
	Brook trout presence (-3.01, 16.48, $P \leq 0.01$)
Columbia spotted frog	
Eggs	Log of lake size (1.611, 10.45, $P \leq 0.01$)
	Lake size (-0.494, 10.45, $P \leq 0.01$)
	Elevation (-0.006, 11.12, $P \leq 0.01$)
	North shore with shallow water and vegetation (0.006, 4.99, $P = 0.03$)
Larvae	North shore with shallow water and vegetation (0.012, 12.5, $P \leq 0.01$)
	Vegetative area (-0.0004, 9.93, $P \leq 0.01$)
	pH (-2.453, 10.48, $P \leq 0.01$)
	Coarse woody debris (-2.126, 9.58, $P \leq 0.01$)

1-30 egg strings were located at individual lakes, although the exact number of egg masses was difficult to determine when there were more than six masses at the same site. Oviposition sites were in shallow water and close to the shore (Table 4). Emergent plants were not a prerequisite, because 47% of the oviposition sites occurred with no emergent plants, and the width of the vegetation averaged 5 m. More than half of the oviposition sites were on the north shore (Table 4) where solar radiation was maximal. Coarse woody debris was present at 73% of the oviposition sites.

There were no significant differences in number of egg strings or larvae between lakes with and without fish (Table 3). The best predictors of toad egg abundance were lake size, water depth, coarse woody debris, and amount of the north shore with shallow water with and without emergent plants (Table 5). Only lake size and coarse woody debris appeared to be indicators of toad larvae by the regression analysis (Table 5). Fish were not good predictors of this species.

Pacific Treefrog

Abundance of Pacific treefrog egg masses was significantly higher in lakes without fish than in lakes with fish ($\chi^2 = 11.38$, $P < 0.01$), although the number of larvae did not differ significantly (Table 3). Of the 32 lakes with treefrog eggs, 21 lacked fish. Eggs were deposited in shallow water

in emergent plants near the shore (Table 4). The average width of the area with emergent plants was 23 m. Eggs occurred in the most extensive patch of emergent vegetation in 75% of the lakes. Coarse woody debris occurred at 55% of the sites with eggs. Half the sites were on the north shore. The abundance of eggs was best predicted by elevation, the absence of brook trout, and the presence of rainbow trout using logistic regression. Abundance of larvae was predicted by pH, log of lake size, and absence of brook trout (Table 5).

Columbia Spotted Frogs

Of the 22 lakes with Columbia spotted frogs egg masses, 11 contained fish. The numbers of egg masses and of larvae at lakes with and without fish were not statistically different. One to three oviposition sites occurred at each lake, with a range of 1 to 135 egg masses. Oviposition sites typically occurred in shallow water close to the shore in emergent plants (Table 4). Ninety-three percent of the oviposition sites were in emergent plants. Oviposition sites occurred in the most extensive patch of emergent vegetation in 75% of the lakes. All shore aspects were used about equally as oviposition sites (Table 4).

Log of lake size, lake size, elevation, and the amount of north shore with shallow water and emergent plants were the best predictors of the abundance of spotted frog egg masses (Table 5). The number of larvae was best predicted by the amount of north shore with shallow water and emergent plants, the size of area with emergent vegetation, pH, and amount of coarse woody debris (Table 5). Fish were not good indicators of this species.

Discussion

Our results indicate that the presence of introduced trout may be detrimental to amphibian biodiversity in high elevation lakes in northeastern Oregon. The lower diversity of amphibians in lakes with fish suggests a negative influence, presumably from fish predation. This negative influence was particularly evident for long-toed salamanders and Pacific treefrogs, while a negative influence of fish could not be detected for western toads and Columbia spotted frogs. High elevation lakes are typically in protected areas where conserving biodiversity and maintaining functioning ecosystems is an objective.

The presence of fish did not significantly influence either reproduction or abundance of larvae of both Columbia spotted frogs and western toads in the lakes we monitored. Habitat conditions were the best predictors of the abundance of both egg masses and larvae of these two species. For the Columbia spotted frog, we suspect the amount of north shore with shallow water and emergent plants and amount of area with emergent plants are particularly important for both eggs and larvae. Emergent plants provide hiding cover from fish. The larvae of Columbia spotted frogs may use the benthic sediment, aquatic plants, and coarse woody debris as refuges. Shallow water on north shores receives the greater solar radiation needed for rapid embryonic and larval development. In July and August, we found larvae in shallow water and typically in the thickest layer of emergent plants that occurred at each lake, which limited exposure to fish.

Our findings differ from several other studies in the western United States. In the Bighorn Crags (Idaho), densities of all life stages of Columbia spotted frogs were lower in lakes with cutthroat trout than in fishless lakes (Pilliod and Peterson 2001). Columbia spotted frogs were typically absent from lakes containing trout in Glacier National Park unless adjacent marsh habitat was present (Marnell 1997). Reaser (2000) suggested that the limited distribution of Columbia spotted frogs in central Nevada resulted from the extensive occurrence of introduced trout. The contrasting results between these studies and the one reported here may be a function of differences in habitat (i.e., amount of emergent plants) at the lakes, species of trout, or landscape characteristics. Stocked lakes in central Idaho may be population sinks in which the persistence of Columbia spotted frogs depends on the number and location of fishless habitats relative to stocked sites (Pilliod and Peterson 2001).

In our study area 11 lakes had both fish and Columbia spotted frogs. Two of these lakes were completely isolated from others. Three of the lakes were within 2 km and downstream of a fishless lake that could have provided recruitment to the lake. The remaining six lakes with fish and spotted frogs were in the same basin with only one fishless lake. It seemed unlikely that the one lake without fish, which contained 25 egg masses, was providing a source population for six other lakes

that each contained 2-47 egg masses. Considering the surrounding watershed or landscape when evaluating the impact of fish stocking is essential to determine if there are sink populations.

Interestingly, degree of isolation (a landscape variable) was not a factor influencing abundance of reproduction in the amphibians in this study. Sixty-three percent of the lakes had streams flowing in and out of them year-round, and another 26% had seasonal streams. Riparian corridors created by these streams may have facilitated dispersal among lakes despite their apparent isolation.

The lack of influence played by fish on toad reproduction was expected based on the known toxicity of the eggs (Licht 1969) and larvae of toad species (Voris and Bacon 1966) to fish. However, Grubb (1972) reported fish predation on eggs of the Gulf coast toad (*Bufo valliceps*) in laboratory tests. Similarly, locations of toads in Rocky Mountain National Park did not differ in habitat conditions or presence of trout (Corn et al. 1997). The majority of toad oviposition sites were on the north shore in shallow water; the larvae congregated in these same areas that lacked emergent plants. Because western toad larvae are toxic to fish, cover may be unnecessary due to the lack of predation. Shallow water provided appropriate thermal conditions for rapid development of embryos and larvae (Brattstrom 1962). At 64% of the oviposition sites, enough coarse woody debris was present between the eggs and the main body of the lake to provide a barrier that protected the eggs from waves on the lake that may have washed them onto the shore. The logs may provide cover for adults from avian and terrestrial predators during oviposition. The association with lake size is explained by the high numbers of egg masses (20-32) and larvae found in the larger lakes (8-35 ha) compared to smaller lakes (<1 ha in size) that contained 1-6 egg masses.

Abundance of the eggs and larvae of both Pacific treefrogs and long-toed salamanders were negatively affected by the presence of eastern brook trout, most likely due to predation. A positive association occurred with rainbow trout and treefrog eggs and salamander larvae, suggesting that the influence of the two trout species differed. Rainbow trout are native to the same region as the amphibians and may be less effective as predators than the exotic eastern brook trout.

First-year long-toed salamander larvae were able to persist in the same lake as trout by using habitats that were inaccessible to trout, like shallow pools, outlets, and dense emergent plants. It appeared that larvae were unable to overwinter in lakes that contained fish because they both would have to overwinter together in the restricted areas of the lake that did not freeze (Pilliod and Peterson 2001)

Other studies have found the detrimental effects of fish on treefrogs and long-toed salamanders. Fish and Pacific treefrog tadpoles did not coexist in high Sierra Nevada lakes; tadpoles occurred in significantly shallower lakes than fish (Knapp and Mathews 2000). A significant negative association existed between fish occurrence and reproduction of long-toed salamanders in the Bighorn Crags of Idaho (Pilliod and Peterson 2001). Long-toed salamanders occurred in a higher percentage of lakes without fish than with fish in the Selway Bitterroot Wilderness of Idaho (Bahls 1990). Sixty-five lakes were surveyed in the Wallowa and Elkhorn Mountains of Oregon in the 1970s, and salamanders occurred only in lakes without fish (James Howard, Humboldt State University, personal communication).

Habitat conditions played little role in predicting the abundance of Pacific treefrogs and long-toed salamanders. Elevation was positively correlated with egg abundance of both amphibians, and a negative association with pH for treefrog larvae. In Colorado, pH decreased significantly with increasing elevation (Corn et al. 1997), so that the association with pH may be a function of elevation.

These findings have major implications because 9,500 of the high elevation lakes in the West and virtually all of the deeper lakes contain introduced salmonids (Bahls 1992). Historically, 95% of these high mountain lakes were naturally fishless prior to stocking (Bahls 1992). Eastern brook trout maintain reproducing populations in some high elevation lakes, and populations exist in lakes that have not been stocked since the 1950s in northeastern Oregon. In contrast, rainbow trout reproduce only if there is a stream with suitable habitat flowing in or out of the lake, so that their populations are not as persistent in most high elevation lakes. If fish disappear from a lake, there is evidence that certain species of amphibians can re-establish their populations in some situations

(Knapp et al. 2001b), although recolonization following extirpation of amphibians from entire basins could take decades (Pilliod and Peterson 2001). The current distribution of trout in high lakes may eventually result in the extirpation of amphibian populations from mountain basins in Idaho, due to a lack of suitable breeding and overwintering habitat in those water bodies that remain fishless (Pilliod and Peterson 2001). Restoring a few deep lakes in each basin to create fishless habitats for breeding and overwintering amphibians has been suggested as one way to conserve biodiversity and maintain a functioning ecosystem in protected areas (Pilliod and Peterson 2001).

If creating fishless habitat is not feasible, protecting or enhancing the emergent plants and coarse woody debris in the littoral zone may improve habitat at ovipostion sites and in areas used by larvae. Livestock graze around some high elevation lakes, and protecting emergent plants with barriers (e.g., coarse woody debris or fencing) at lakes with fish would help retain hiding cover at these lakes. The introduction of coarse woody debris into shallow zones may increase the hiding cover for larvae, reduce exposure to trout, and reduce effectiveness of fish as predators during the summer.

Acknowledgements

Thad Heater, Janet Hohmann, and Dave Wyland assisted with field work. Jay Shepherd assisted with statistical analyses. An earlier draft of the manuscript was reviewed by Phil Howell, Bryce Maxell, and Barb Wales. Oregon Department of Fish and Wildlife provided information on lake size and stocking records. Funding was provided by U.S. Fish and Wildlife Service and Pacific Northwest Research Station.

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Received 28 November 2001
Accepted for publication 28 January 2002

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Jeffrey R. Dunk,[1] Redwood Sciences Laboratory, Pacific Southwest Research Station, USDA Forest Service, 1700 Bayview Drive, Arcata, California 95521 and Department of Natural Resources Planning and Interpretation, Humboldt State University, Arcata, California 95521

William J. Zielinski, Redwood Sciences Laboratory, Pacific Southwest Research Station, USDA Forest Service, 1700 Bayview Drive, Arcata, California 95521

Karen West, Klamath National Forest, 1312 Fairlane Road, Yreka, California 96097

Kristin Schmidt,[2] Six Rivers National Forest, 1330 Bayshore Way, Eureka, California 95501

Jim Baldwin, USDA Forest Service, Pacific Southwest Research Station, Albany, California

Julie Perrochet, Klamath National Forest, 1312 Fairlane Road, Yreka, California 96097

Kary Schlick,[3] Humboldt State University Foundation, Humboldt State University, Arcata, California 95521

and

Jan Ford, Klamath National Forest, 1312 Fairlane Road, Yreka, California 96097

Distributions of Rare Mollusks Relative to Reserved Lands in Northern California

Abstract

In 1994 the Northwest Forest Plan identified several hundred relatively rare plant and animal species as "Survey and Manage" based in part on their presumed association with late-successional/old-growth forests. Other such species were given protection from grazing. However, broad-scale surveys for few of these species existed at that time. In 1999-2000 we evaluated the relationship of nine terrestrial mollusks to U. S. Forest Service reserves in four National Forests in northern California. The nine mollusks were well distributed among reserved and non-reserved lands and showed no association with Late Successional Reserves, Congressionally Reserved, Administratively Withdrawn, or Matrix land allocations. However, the mollusks occurred more frequently than expected in Riparian Reserves when all other land allocations were combined. Our results are a step toward evaluating the protection that the Northwest Forest Plan affords these mollusks in northern California.

Introduction

Survey and Manage (S&M) species are thought to be rare, or their geographic ranges or habitat associations were not sufficiently known at the time of the Northwest Forest Plan (NWFP) to determine whether reserved lands would adequately protect their populations (USDA/USDI 1994). Furthermore, other species were given protection from grazing under the NWFP; some of these have subsequently been put on the S&M list. In northern California, all or part of six National Forests exist within the range of the northern spotted owl (*Strix occidentalis caurina*), which delineates the boundaries of the NWFP. Within four of these forests (Shasta-Trinity, Klamath, Six Rivers, and Mendocino), nine terrestrial mollusks were selected for study because of their protection under the NWFP. They were selected on the basis of three criteria: (1) the belief that they existed on more than one of the four forests; (2) the requirement to survey them prior to timber harvest or other land-disturbing activities; and (3) the implications of their discovery for local land management planning (e.g., interference with scheduled applications of prescribed fire or fuel reduction activities). The subset of species selected included: the hooded lancetooth (*Ancotrema voyanum*), Oregon shoulderband (*Helminthoglypta herleini*), Klamath shoulderband (*H. talmadgei*), chace sideband (*Monadenia chaceana*), Church's sideband (*M. churchi*), Klamath sideband (*M. fidelis klamathica*), yellow-based sideband (*M. f. ochromphalus*), pappilose tail-dropper (*Prophysaon dubium*), and Tehama chapparal (*Trilobopsis tehamana*). Little published information exists on the habitat relationships or geographic range of any of these species. Roth and Pressley (1986)

[1] Address to whom correspondence should be addressed. E-mail: jdunk@fs.fed.us

[2] Current address: Redwood National and State Parks, P.O. Box 7, Orick, CA 95555

[3] Current address: Six Rivers National Forest, 1330 Bayshore Way, Eureka, CA 95501

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mentioned the range of *M. churchi* along with general habitat associations and Cameron (1986) evaluated associations between mollusks and environmental variation in British Columbia. *Monadenia fidelis* occurred in Cameron's study area, but not the subspecies with which we were concerned.

The NWFP incorporated seven land allocations, five of which we evaluated. Congressionally Reserved Areas (CR) were lands set aside for specific purposes by Congress, such as National Parks, Wilderness Areas, and Wild and Scenic Rivers. The NWFP did not alter any pre-existing mandates on these lands. Late Successional Reserves (LSR) were designated in the NWFP to serve as, or become habitat for, late-successional and old-growth related species. Administratively Withdrawn Areas (AWA) were areas identified in National Forest plans to include visual areas, back country, and other areas not scheduled for timber harvest. Riparian Reserves (RR) were designated to protect aquatic species/habitats, and to connect late-successional habitats. RR occur in every other land allocation within a specified distance of streams (see below). Matrix is all land outside of all other categories, and represents the land in which the majority of timber harvest and silviculture activities occur (USDA/USDI 1994). The two allocations we did not evaluate, Adaptive Management Areas (AMA) and Managed Late Successional Reserves (MLSR), were not conducive to this analysis owing to their overlying other land allocations (AMA) or their small size (MLSR; <1% of the land area).

The degree to which currently reserved lands support long-term persistence of these mollusk species is of considerable interest. For instance, if the majority of the mollusk species are associated with LSR, one might conclude that the existing habitat for such species occurs only in LSR or that these reserves are adequately protecting such species. If the species are found in LSR and Matrix lands, however, we might conclude that the species are broadly distributed and do not need protections they are currently afforded, or that their habitat needs are not provided by LSR and additional habitat protection in Matrix lands may be warranted. For the second interpretation, it could be that rare habitat features required by a species are not primarily found in LSR.

Our project objectives were to 1) evaluate the distribution of these mollusks relative to reserved lands; 2) estimate the geographic range of each species; and 3) attempt to develop empirical models to predict each species' presence-absence throughout the study area. Herein we present our findings for the first objective.

We tested the null hypothesis that one or more of the selected mollusks occurred proportionately among land allocation types against the alternate hypothesis that these mollusks were represented disproportionately in one or more land allocations. We were especially interested in the degree of association of the mollusks to reserved lands relative to non-reserved lands.

Methods

The study area included the Klamath, Mendocino, Shasta-Trinity, and Six Rivers National Forests in northern California (Figure 1). These forests encompass >2.2 million ha of primarily forested habitat. Mollusk surveys were conducted at Forest Inventory and Analysis (FIA) plots during 1999 and 2000. The FIA program is national in scope and is designed to inventory and monitor change in forest composition and structure (White et al. 1992, USDA 2000). FIA plots occur on a grid with 5.4 km between points. Each plot is ~1 ha and contains five 0.1-ha subplots where detailed information on live and dead vegetation is collected (USDA 2000). Mollusks were surveyed at 307 FIA points randomly selected from 1055 plots on the 5.4 km grid available on the four National Forests.

Owing to the paucity of existing information on the selected mollusks, we stratified our sampling by allocating plots proportionate to each National Forest's area so we would not randomly under-sample any forest. Because of a keen interest in the association of the selected species with RR, we ensured that the number of points that occurred in RR was proportionate to the area of RR. This required the addition of four RR plots on the Six Rivers and six RR plots on the Shasta Trinity National Forests. Riparian Reserves were identified using a geographic information system that used USGS cartographic feature files from the US Forest Service Remote Sensing Laboratory in Sacramento, California. Fish-bearing streams were identified by state and federal fisheries biologists in 1995. Fish-bearing streams were buffered 90 m on each side and non-fish bearing streams were buffered 45 m on each side as required by the USDA/USDI (1994).

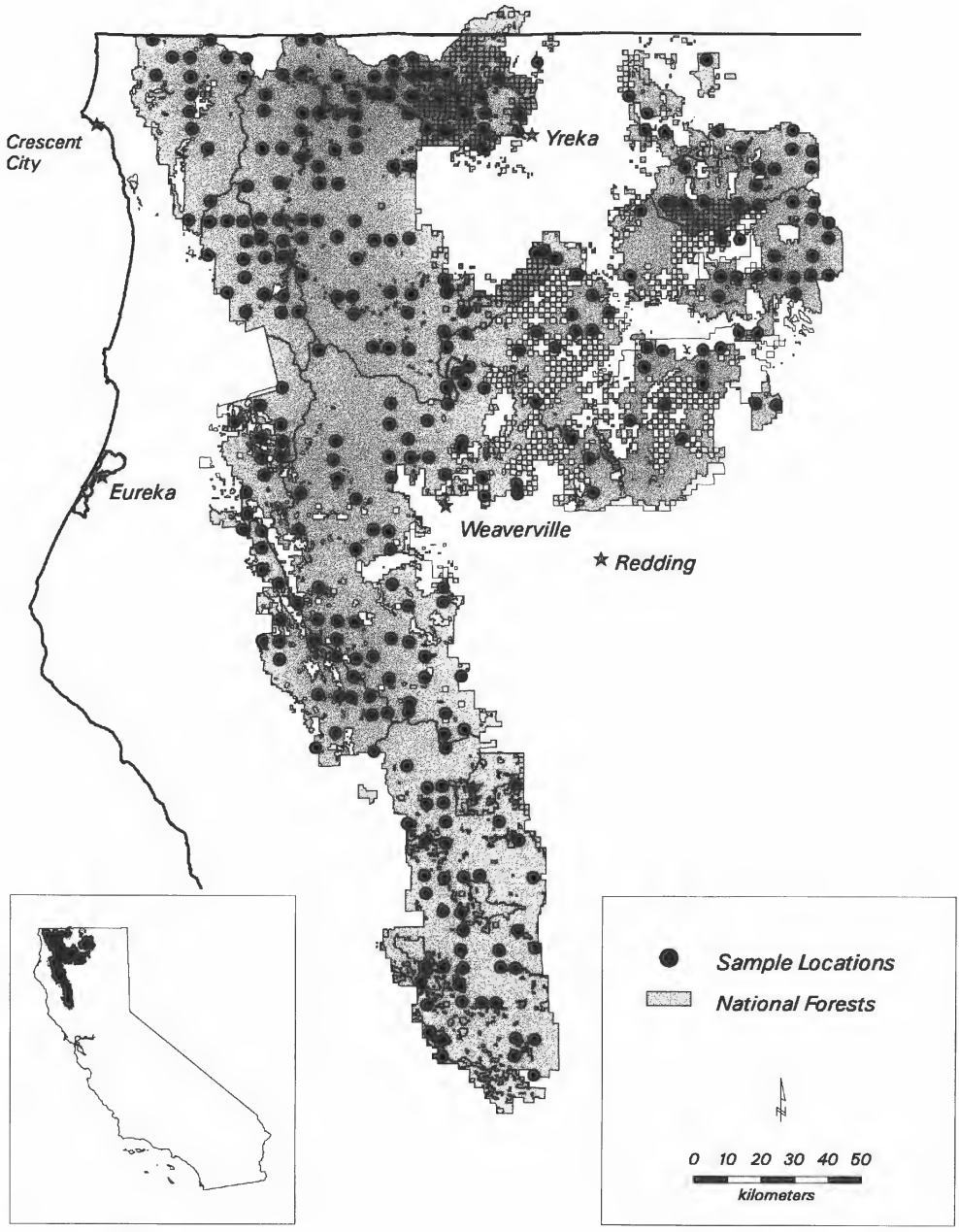

Figure 1. Study area location and distribution of sampling locations.

Mollusks were sampled between March 1999 and September 2000 on the Klamath National Forest, and between 10 April 2000 and 1 July 2000 on the other three National Forests. Each selected FIA point was sampled twice, with a minimum of 10 days between the first and second surveys. Our survey protocol was modified from the protocol currently used for pre-project surveys. We collected many more micro- and macro-habitat variables (for future development of habitat models) than the standard protocol and we also increased the survey effort from one person-hr/4 ha to one person-hr/1 ha.

Surveys were conducted only if the daytime temperature was >5° C and soil was moist as determined by touch. Surveys began with crews walking through the plot and identifying structural features that were likely to provide mollusk habitat (e.g., downed wood), after which two types of focused searches were conducted. Area searches targeted the most likely mollusk habitat by thoroughly inspecting all features and the area likely to conceal them within a radius of 5 m (i.e., 80 m^2) surrounding that feature. One 20-min time-constrained area search was conducted. Point searches were 40-min time-constrained searches, but unlike area searches they were opportunistic searches not constrained to a small area. Surveyors went from one point to another, but were limited to a maximum of 3 min at any one point before moving on to another point. We did not estimate the abundance of each species.

Because of the difficulty of distinguishing species in the field, a single specimen of each putative species (live if available, shell if that was all that was found) was collected from each plot for laboratory identification. Field collected specimens were given to staff experienced in mollusk identification at the Klamath, Mendocino, and Six Rivers National Forests and to one independent contractor, called Second Level Identification staff. If the Second Level Identification staff could not confidently identify a specimen, the specimen was forwarded to Dr. Barry Roth, an expert in mollusk taxonomy, for identification.

We used chi-square tests to evaluate the relationships of mollusk presence to land allocation type. If, as under the null hypothesis, no association between land allocation and the presence of one or more of the mollusks exists, the expected number of detections of mollusks in each land allocation category should be equal to the total number of plots in which mollusks were found multiplied by the proportion of sampled plots within each land allocation category. Recall that the response at each FIA plot is binary (0, 1); either none (0) or one or more (1) of the selected mollusks was found, regardless of the number of species or the number of individuals of each species that were observed. Chi-square tests should not be conducted using the χ^2 distribution approximation when more than 20% of the categories contain expected frequencies ≤5 (Zar 1999). For this reason, and because the detection of any one species at a proposed project area calls for additional review of the management activity, we treated our set of species as a group. However, for descriptive purposes we also provide data for individual species.

Each crew, usually composed of two people, received similar training. Nonetheless, we were interested in evaluating among-crew variation in detecting one or more of the selected species. To do so, we randomly selected 30 plots that would be sampled by a second crew that was unaware of the results of the initial crew. We compared the proportion of plots in which the two different crews arrived at the same conclusion regarding the presence or absence of any of the nine species. We used McNemar's test for paired-sample nominal scale data (Zar 1999) to compare the results of the two initial visits to the same plots by separate crews. The individual species were not of interest in this evaluation, only whether there was agreement in the detection (or lack of detection) of one or more of the selected mollusk species. Our evaluation of the among-crew sampling variation revealed that different crews achieved the same overall proportion of presence (McNemar's χ^2 test statistic = 0.14286—with no continuity correction), but 23% (7) of the 30 test plots differed in the assessment of presence, thus there appears to be no crew bias for the overall proportion of presence.

Results

Of the 307 plots sampled, 153 were in Matrix (49.8%), 76 in LSR (24.8%), 58 in CR (18.9%), 20 in AWA (6.5%). Forty sample plots (13.0%) occurred within RR. One or more of the nine mollusks were found at 113 of the 307 plots (36.8%) (Figure 2). Individual species were detected at

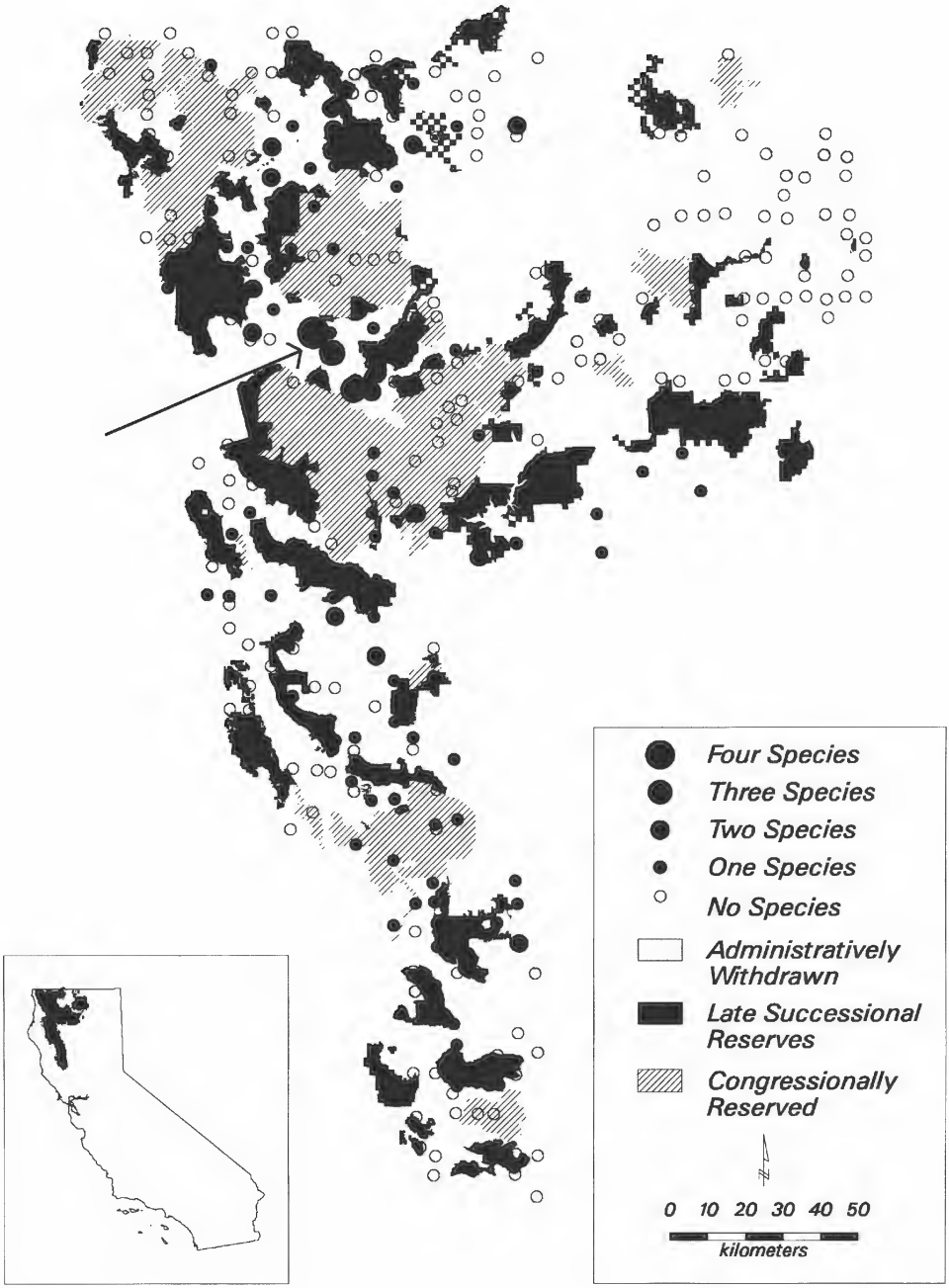

Figure 2. Sampling locations and the presence of the selected mollusk species relative to land allocation status. The arrow points toward the area with high rare mollusk species richness.

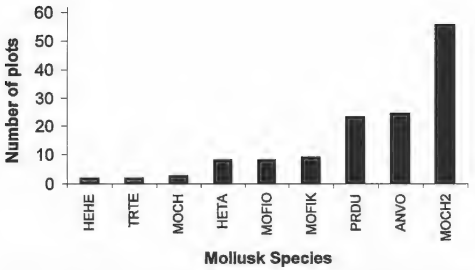

Figure 3. Number of sampling locations at which each of the selected mollusk species was detected. Four letter acronyms refer to the following species: ANVO = *Ancotrema voyanum,* HEHE = *Helminthoglypta herleini,* HETA = *H. talmadgei,* MOCH = *Monadenia chaceana,* MOCH2 = *M. churchii,* MOFIK = *M. fidelis klamathica,* MOFIO = *M.f. ochromphalus,* PRDU = *Prophysaon dubim,* and TRTE = *Trilobopsis tehamana.*

from 2-55 plots (Figure 3, Table 1) and six of the nine species were detected at less than 10 plots.

We failed to reject the hypotheses that the proportion of samples with at least one focal mollusk species detection was equal among the four forests ($\chi^2 = 1.811$), and thus did not further subdivide analyses by forest/strata. When evaluating the association of mollusks with Matrix, LSR, CR, and AWA land allocations, no significant association was found (Table 2, Figure 3). This analysis, however, did not consider RR as a separate land allocation because this allocation is often viewed as an overlay over all other land allocations, effectively superseding other more liberal land use practices that might exist. When we included RR as a separate land allocation, we found

TABLE 1. Detections of individual selected mollusk species by land allocation status. LSR = Late Successional Reserves; CR = Congressionally Reserved; AWA = Administratively Withdrawn Areas.

	Matrix	LSR	CR	AWA	Total
FIA plots sampled	153	76	58	20	307
Proportion of total	0.50	0.25	0.19	0.07	
Ancotrema voyanum					
Number	10	9	3	2	24
Proportion	0.42	0.38	0.13	0.08	
Helminthoglypta herleini					
Number	0	1	0	1	2
Proportion	0.00	0.50	0.00	0.50	
Helminthoglypta talmadgei					
Number	6	0	1	1	8
Proportion	0.75	0.00	0.13	0.13	
Monadenia chaceana					
Number	2	1	0	0	3
Proportion	0.67	0.33	0.00	0.00	
Monadenia churchii					
Number	26	14	11	4	55
Proportion	0.48	0.26	0.20	0.07	
Monadenia fidelis klamathica					
Number	6	3	0	0	9
Proportion	0.67	0.33	0.00	0.00	
Monadenia fidelis ochromphalus					
Number	5	2	0	1	8
Proportion	0.63	0.25	0.00	0.13	
Prophysaon dubium					
Number	12	6	3	2	23
Proportion	0.52	0.26	0.13	0.09	
Trilobopsis tehamana					
Number	2	0	0	0	2
Proportion	1.00	0.00	0.00	0.00	

TABLE 2. Results of χ^2 analysis of associations between mollusks and land allocations. LSR = Late Successional Reserves; CR = Congressionally Reserved; AWA = Administratively Withdrawn Areas; RR = Riparian Reserves.

	Matrix	LSR	CR	AWA	RR	χ^2	*P*
	Selected mollusks by four land allocations						
Observed number	54	33	17	9			
Expected number	56.3	28.0	21.3	7.4		2.249	0.522
	Distribution of sample locations among five land allocations						
Observed number (307)	139	62	51	15	40		
Observed proportion	0.453	0.202	0.166	0.049	0.130		
	Selected mollusks by five land allocations						
Observed number	46	25	12	8	22		
Expected number	51.2	22.8	18.6	5.5	14.7	7.88	0.096

TABLE 3. Results of χ^2 analysis comparing mollusks on Riparian Reserves (RR) and Late Successional Reserves (LSR) against other land allocations.

	RR	LSR	Other	χ^2	*P*
Riparian Reserves vs. Other land allocations					
Observed number	22		91		
Expected number	14.7		98.3	4.202	0.040
Late Successional Reserves vs. Other land allocations					
Observed number		33	80		
Expected number		28.0	85.5	1.198	0.274

a stronger association between presence of the mollusks and land allocation status (Table 2). We also compared the association of one or more of the mollusk species with RR versus all other land allocations as a group. Mollusks were found at 22 of the 40 RR plots (55%). Under the null hypothesis of no association with RR, the expected number of plots with mollusks in RR was 14.7, which resulted in a significant association with RR (Table 3). We found no association between the presence of one or more of the mollusks in LSR versus other land allocations (Table 3) or when comparing reserved (i.e., LSR, CR, AWA, and RR) versus Matrix lands. Analyses were also conducted excluding *Prophysaon dubium* (detected at 23 plots) because this slug may be a habitat generalist and not need S&M protection (USDA/USDI 2001). However, excluding *P. dubium* did not appreciably alter the results.

Discussion

As a group, the selected mollusks in our study only showed an association with RR. This conclusion should be moderated, however, by the knowledge that one less observation of presence would have yielded a non-significant *P*-value of 0.076 (using the conventional alpha level of 0.05); and two fewer observations would have yielded a *P*-value of 0.136. In addition to the purpose of providing protection to aquatic organisms/habitats (USDA/USDI 1994), RR were also envisioned to provide connectivity among habitat patches. We believe that it is premature to draw any conclusions about the need for more or less protection, or about the importance of any habitat feature for this group. This requires species-by-species habitat analyses, which we plan to conduct, before a more complete picture of the distribution and habitat associations of each species will be possible. The general lack of association of the selected species with reserved lands, however, suggests that the conservation of these species will require careful management of Matrix lands. For example, the geographic ranges of *M. f. klamathica* and *M. f. ochromphalus* are extremely small and most of the detections were in Matrix. When appropriate habitats are identified for each species, especially those with small geographic ranges, evaluating distributions of habitat by land allocations will be of great interest. Furthermore, the relative concentration of high species richness of the selected species (Figure 2) occurs primarily in Matrix lands. Until individual species distributions are evaluated relative to their habitat associations and reserve status, we recommend continuing pre-project surveys.

Acknowledgements

We would like to thank J. Werren for producing the maps, A. Albert for editorial assistance, and B. Howard and D. LaPlante for database management assistance. We also thank D. McKenzie and N. Duncan for helpful comments on an earlier draft, and B. Roth for identifying many specimens and providing helpful comments on a draft of the manuscript. We also wish to thank the Pacific Southwest Research Station and the Six Rivers, Shasta-Trinity, Klamath, and Mendocino National Forests for supporting this project. We also thank J. Applegarth for reviewing the manuscript and providing helpful comments. This work was funded by the Pacific Southwest Research Station and the Klamath National Forest.

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Received 12 June 2001
Accepted for publication 1 February 2002

Northwest Science Notes

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Mary F. Fauci[1] and **David F. Bezdicek,** Department of Crop and Soil Sciences, Washington State University, Pullman, Washington 99164-6420

Lumbricid Earthworms in the Palouse Region

Abstract

Farmers, gardeners, and ecologists view earthworms as beneficial soil organisms indicative of healthy soils. Earthworms in the Palouse region of eastern Washington and northern Idaho have not been well documented. Since the early 1900s, most of the Palouse had been converted to dryland farming except for intermittent streams and areas too rocky to till. We surveyed 46 sites in spring 1999 to determine the occurrence and distribution of earthworm species within the agricultural landscape. Although species diversity in the agricultural fields was low, three species are reported in the survey area for the first time. No native earthworms were found. Ten alien lumbricid species were found. The most common, *Aporrectodea trapezoides*, was found at 65% of all sites. Of the farmed field sites, 61% contained one or more species. This preliminary survey provides the baseline knowledge necessary to design future studies on earthworms.

Introduction

The distribution of earthworms (Annelida: Oligochaeta) of the Palouse region of eastern Washington and northern Idaho is largely unknown (James 2000). The Washington giant earthworm (*Driloleirus americanus*: Megascolecidae) is the only native worm known from the area (James 2000). Intensive tillage and conversion of steppe grasslands to annual small grain cropping have greatly reduced the habitat for *D. americanus* (Black et al. 1998), which was last collected in 1978 (Wells et al. 1983).

Most earthworms found in the Palouse are members of the family Lumbricidae, all of which are thought to be introduced from Europe (James 2000). Land use and management practices can affect earthworms (Chan 2001). For example, summer-fallow is a tillage-intensive, agricultural practice whereby no crop is grown and the soil is void of surface residues for up to 16 mo out of every two-year cropping cycle. Typically eight or more tillage operations occur during a fallow period. Even where fallow is not practiced, reducing tillage can improve habitat for earthworms (Chan 2001). Recently there has been increased adoption of no-till or direct seed practices by farmers in the region who are concerned about the health and quality of their soil. These farmers equate healthy earthworm populations with high quality soil. Some Palouse farmers who seed directly without tillage often observe abundant populations of earthworms, yet others are disappointed that their fields do not contain earthworms. They expect earthworms to become abundant when they cease tilling, but absence of worms may reflect ecological (worms cannot exist there) or zoogeographical (worms have not yet arrived) causes (Reynolds 1998).

We documented earthworm species at 46 sites in and around the Palouse region of eastern Washington and northern Idaho in spring 1999. Our objective was to determine the occurrence and distribution of earthworm species in the area, focusing on the agricultural landscape in the Palouse

[1] Author to whom correspondence should be addressed. E-mail: mfauci@wsu.edu

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region. James (2000) summarized the distribution of earthworm species in the broader ecoregion of the Columbia Basin, based on earlier surveys reported by Fender (1985). We thought more specific and recent observations were needed on species distribution of worms in local fields to address farmer's concerns.

Study Area and Methods

The study area included the Washington and Idaho Palouse and adjoining areas (Figure 1). Most of the native shrub steppe vegetation of the area has been converted to agriculture, predominantly dryland wheat (Black et al.1998). We sampled 46 sites. Most were located in fields with a history

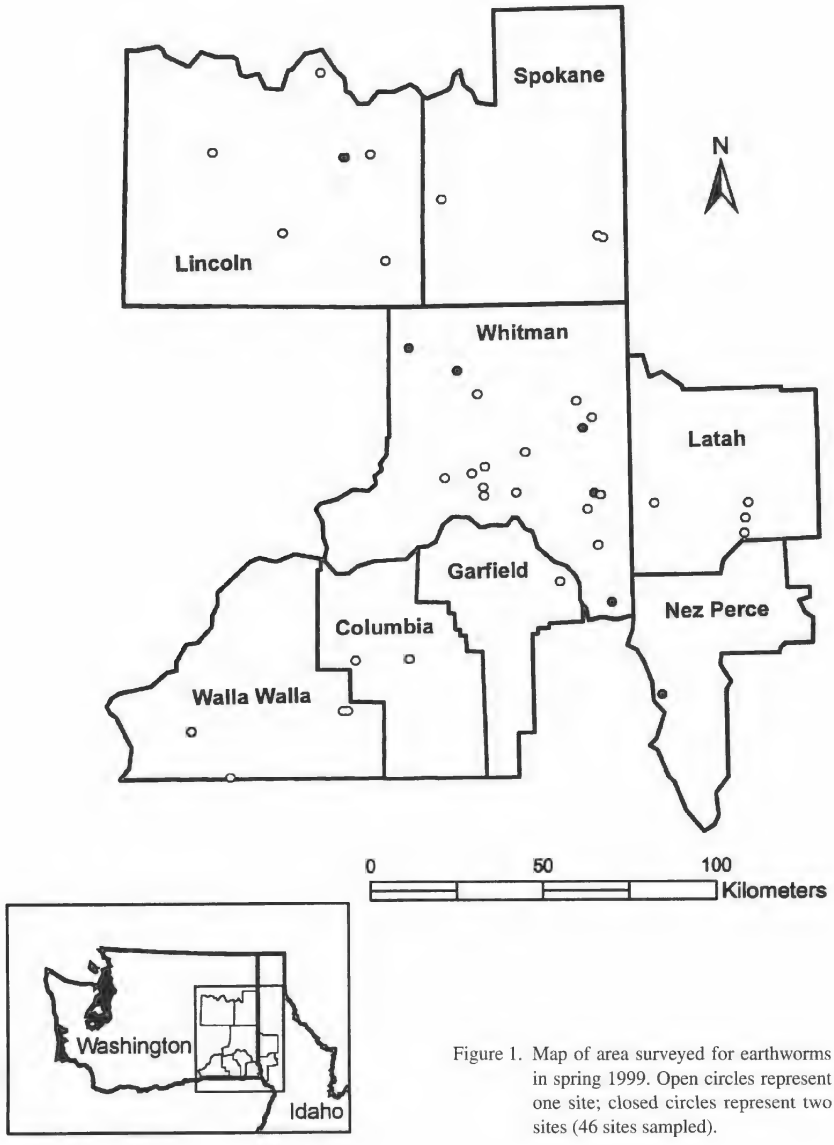

Figure 1. Map of area surveyed for earthworms in spring 1999. Open circles represent one site; closed circles represent two sites (46 sites sampled).

of conservation tillage where we knew the farmer (n=*29*). As we traveled from field to field, we sampled other sites that we thought might support earthworms. These sites were adjacent to waterways, in perennial vegetation, along road rights-of-way, or old homesteads (n=*17*).

We collected worms from February to May 1999. At each sample site, we dug, hand-sorted, and examined six spades of soil for worms. These six samples were distinct and randomly located within a 10-m^2 area. If immature worms were found we continued sampling to find adults with developed clitella for positive identification. Live adult worms were transported to the lab for identification. We identified worms based on external morphology of sexually mature specimens using keys by Schwert (1990) and Fender (1985). Nomenclature followed Fender (1985).

Results

We did not find *Dendrodrilus americanus*, but we found 10 lumbricid species during our survey (Table 1). *Aporrectodea trapezoides*, the most common species, was found at 65% of all sites. In the agricultural field sites we found four species, three of which were in less than 15% of the fields. Diversity in the agricultural field sites was low. Of the 29 agricultural field sites, 11 lacked worms, 11 had one species, 6 had two species, and 1 had three species.

The Washington State University campus had the greatest worm diversity with eight species found in the agronomy teaching garden. Of the 10 species detected in our study only *Eiseniella tetraedra* and *Allolobophora chlorotica* were not found at this site. Species diversity was also high adjacent to waterways or in low-lying pastures. In early July 2000, *A. chlorotica* was identified adjacent to a seasonal waterway at one of the sites surveyed in 1999. That site had six worm species. Two other pasture sites each had five species.

Aporrectodea rosea, *Dendrodrilus rubidus*, and *Octolasion cyaneum* were detected for the first time in our study area (Table 2). *Aporrectodea rosea* was found in five of the survey locations, on campus, along streams, and in pastures. *Dendrodrilus rubidus* was found in a pasture adjacent to a perennial creek and under straw in the agronomy garden on campus. *Octolasion cyaneum* is common on the WSU campus. Other species reported by previous investigators (Fender 1985, James 2000) that we did not find were *L. rubellus* and *O. tytraeum* (Table 2).

TABLE 1. Species occurrence (%) at all sites, in agricultural field sites, and in the other sample locations (adjacent to creeks, rights-of-way, pastures, and campus).

Species	All sites (n=46)	Agricultural field sites (n=29)	Other sites (n=17)
Aporrectodea trapezoides	65	55	82
Aporrectodea tuberculata	28	10	59
Lumbricus terrestris	24	14	41
Aporrectodea turgida	20	10	35
Aporrectodea rosea	11	0	29
Dendrodrilus rubidus	4	0	12
Eiseniella tetraedra	2	0	6
Allolobophora chlorotica	2	0	6
Eisenia fetida	2	0	6
Octolasion cyaneum	2	0	6
No worms	24	38	0

TABLE 2. Lumbricid worm species found in this and previous surveys (Fender 1985, James 2000).

Species	Spring 1999 survey	Previous surveys
Allolobophora chlorotica	+	+
Aporrectodea rosea	+	
Aporrectodea trapezoides	+	+
Aporrectodea tuberculata[1]	+	+
Aporrectodea turgida	+	+
Dendrodrilus rubidus	+	
Eiseniella tetraedra	+	+
Eisenia fetida	+	+
Lumbricus terrestris	+	+
Lumbricus rubellus		+
Octolasion cyaneum	+	
Octolasion tytraeum		+

[1] referred to as *Allolobophora tuberculata* in James (2000).

Discussion

The presence or absence of lumbricid worms in agriculture fields is probably related to a combination of past livestock practices, homesteads, proximity to watercourses, climate, and soil management. No worms were found at 11 of the 29 agricultural field sites. Nine of these were clustered in the northwest corner of the survey area, in western Whitman and Spokane Counties and all of the sites in Lincoln County. Summer fallow was practiced extensively in this area in the

past, although recently more growers direct seed, without any tillage. Our survey sites in this area had been under direct seed management for a minimum of four years. These sites are located in an area that is as dry as many of the sites that have worms, but it is colder. Perhaps worms cannot survive these conditions or they have not arrived yet. An adjacent abandoned homestead harbored both *Aporrectodea trapezoides* and *A. tuberculata*.

Two other field sites without worms included a shallow soil in southern Whitman County on the breaks of the Snake River and a deep coarse soil in Touchet, western Walla Walla county (Figure 1). The shallow soil dries completely to bedrock each summer. Earthworms persist in dry environments by burrowing deeply into moist soil or aestivating during drought. Thus, refuge from dry conditions may not exist at this site. Although the soil is deep in Touchet, the lack of moisture (less than 250 mm rain per year) and coarser soil texture may explain the absence of worms at that site. These sites might support worms if they were introduced.

The locations chosen and timing of our survey influenced the results. For example, in midsummer, July 2000, we found an additional worm species (*Allolobophora chlorotica*) at a site we had surveyed in early spring. Perhaps juveniles of this species were present during our spring sampling, but we found no adults. Worm species that live in permanent deep burrows, like the night crawler (*Lumbricus terrestris*) can escape shallow sampling by withdrawing into their burrows. We checked sites with large diameter worm burrows (greater than 6 mm) carefully because *D. americanus* is believed to inhabit permanent or semi-permanent deep vertical burrows (James 2000) much like *L. terrestris* and adults of both species are of similar diameter. However, at all sites with large diameter burrows, we found adult *L. terrestris*.

Acknowledgments

We thank Richard Repp for GIS support and the Vogel Grant for financial support.

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Received 11 June 2001
Accepted for publication 1 February 2002

Michael D. Pope[1], **Nathaniel Richardson,** and **John A. Crawford,** Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, Oregon 97331-3803

Fall and Winter Diets of Mountain Quail in Southwestern Oregon

Abstract

Ninety mountain quail crops were collected in the fall of 1994-96 and the winter of 1998-99 to determine diets of mountain quail in the southwestern Cascade Mountains of Oregon. Mountain quail consumed items from 61 plant taxa, but the bulk of their diet was composed of 13 major plant genera or species. Legumes were the most prominent food consumed by Mountain Quail. In the fall, deervetch species accounted for 47% of the total dry weight and were found in 58% of the crops. Hairy vetch constituted 38% of the dry weight of crops collected during the winter and occurred in 50% of the crops. Other legumes commonly eaten during the fall were black medic, clover, peavine, and Scot's-broom. California hedge-parsley, manzanita, and hawthorn were frequently used in the winter. Mountain quail ate greater quantities of grasses and green foliage in the winter, but berries were consumed more during the fall. In fall and winter, insects were frequently found in crops, but composed ≤3 % of the total volume of the diet. Mountain quail in southwestern Oregon are opportunistic foragers that seasonally shift diets to take advantage of prevailing food abundances.

Introduction

Mountain quail (*Oreortyx pictus*) occupy a diverse range of Pacific Coastal and Great Basin habitats from Baja, Mexico to Washington. They are highly herbivorous, and opportunistically exploit temporarily abundant food sources (Gutiérrez 1977). Mountain quail in central coastal California consumed 130 different food resources that consisted primarily of fruits, flowers, seeds, bulbs, or other plant parts (Gutiérrez 1977). However, mountain quail predominantly selected perennials, and >60% of the diet in central coastal California was composed of only six genera: woodlandstar (*Lithophragma*), oak (*Quercus*), starwort (*Stellaria*), filaree (*Erodium*), clover (*Trifolium*), and sumac (*Rhus*). In southeastern Washington, 85 of 95 food items collected from mountain quail crops and gizzards during the fall were plants, but >50% of the food biomass consisted of seven plant species (Yocum and Harris 1953). Mountain quail crops collected in western Idaho in the fall contained >37 different plant species, but four species accounted for >70% of the crop contents (Ormiston 1966).

Seasonally, mountain quail shift diets and foraging strategies to take advantage of prevailing food abundances. Chickweeds (*Holosteum* spp.) were important spring and early summer foods for mountain quail in western Idaho, but after August these species were rarely found in crops (Ormiston 1966). In western Idaho, mountain quail diets changed from the seeds of small annuals in the summer to the seeds of larger perennials and annuals in September and October (Ormiston 1966). Mountain quail are sequential specialists with a diverse foraging repertoire that includes digging for bulbs in the fall, climbing trees to gather seeds, jumping to collect seeds from flower stalks, and shelling acorns found on the ground (Gutiérrez 1977).

Mountain quail are distributed throughout the western Cascades of Oregon, generally from 600 to 1,800 m elevation. In the Cascades of southwestern Oregon, mountain quail are abundant and occupy diverse habitats including many early, seral shrub and mixed-forest communities (Steve Denney, Oregon Department of Fish and Wildlife, personal communication). No studies have examined diets of mountain quail in the predominantly mesic, coniferous forests in the western Cascades. The objectives of our research were to understand mountain quail diets in the western Cascades, particularly during fall and winter when food resources are patchy in distribution and less abundant. We hypothesized that mountain quail in southwest Oregon would use a diverse range of plant species, but the bulk of their diet would consist of a few seasonally abundant species. We predicted that from fall to winter, consumption of particular food items would shift as food resources declined in quantity and variety.

[1]Author to whom correspondence should be addressed.
E-mail: popem@onid.orst.edu

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Methods

Study Area and Data Collection

We selected a 1,400-km^2 study site in the Cascade Mountain Range of southwestern Oregon. The area, 50 km southeast of Roseburg in the Umpqua National Forest, is characterized by dense forests with floristically diverse forest overstories dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and other conifers, or by Oregon white oak (*Quercus garryana*) and Pacific madrone (*Arbutus menziesii*) (Franklin and Dyrness 1988). Common understory shrubs include manzanita (*Arctostaphylos* spp.), ceanothus (*Ceanothus* spp.), vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), poison oak (*Rhus diversiloba*), and Oregon grape (*Berberis* spp.). Historically, fires, both naturally caused and set by native Americans, were the greatest single influence that created and perpetuated plant communities (Franklin and Dyrness 1988). Currently, logging is the major disturbance factor. Extensive timber removal on public and private lands has resulted in a mosaic of early to late-successional forest habitats. Elevations range from 600 to 1,800 m and climate conditions are generally temperate with hot, dry summers and cool, moist conditions in fall, winter, and spring. Mean monthly temperatures in 1999 ranged from 9°C in January to 29°C in August and annual precipitation was 76 cm (Oregon State University Climate Service 1999).

Sixty-one mountain quail were collected from the study area by hunters and Oregon Department of Fish and Wildlife biologists during the fall (1 September-1 December) of 1994 to 1996. Twenty-nine mountain quail were collected during the winter (2 December to 1 March) of 1998 and 1999. To insure independence of samples, we required that hunters collect one bird per covey. Crops were removed, and the contents extracted and dried in an oven at 50°C for 24 hr. Dried crop contents from each bird were sorted, weighed, and identified. Procedures for identification included photographic-key manuals, visual comparisons to seed collections, and assistance from Oregon State University's Seed Laboratory. Insect parts were sent to the Department of Entomology at Oregon State University for identification. Frequency of occurrence for each crop item was determined by recording the total number of birds that consumed that item. Percent dry weight was determined by dividing summed weights for each item by the total weight of crop contents. We compared species composition, frequency of occurrence, and dry weight of fall and winter crop contents to assess seasonal shifts in diet selection.

Results

Mountain quail crops collected during the fall consisted of items from 24 plant taxa. Seeds were the most used food and composed the greatest biomass (dry weight) of crop contents (Table 1). Legumes were the most common family represented in mountain quail crops, and were 47% of the total dry weight (Table 2). Deervetches (*Lotus* spp.) were found in 35 of 61 (58%) of the crops, and accounted for 18% of the dry weight of all crops. Other common legumes in crops were black medic (*Medicago lupulina*), vetches (*Vicia* spp.), clover (*Trifolium* spp.), Scot's-broom (*Cytisus scoparius*), and peavine (*Lathyrus* spp.). Tarweed (*Madia* spp.) was found in 25% of crops but was only 2% of the total dry weight. Tall fescue (*Festucca arundinacea*), dogtail's grass (*Cynosurus echinatus*), blackberries (*Rubus* spp.), and snowberries (*Symphoricarpos* spp.) were frequently used (Table 2). Insects (termites, butterflies, earwigs, ants, grasshoppers, beetles, bugs, and spiders) from eight orders (*Isoptera*, *Lepidoptera*, *Dermaptera*, *Hymenoptera*, *Orthoptera*, *Coleoptera*, *Hemiptera*, and *Araneae*) were found in 45 of 61 (73%) of crops, but constituted 3% of the dry weight, and likely were only incidentally consumed. Unidentified green herbage was found in 15 of 61 (26%) of crops, but accounted for <2% of dry matter weight. Bulbs occurred in only 5 of 61 (8%) of the crops.

TABLE 1. Percent dry weights of major diet categories found in mountain quail crops (n = 90) collected in fall of 1994-96 and winter 1998-99 in the Cascade Mountains, southwestern Oregon.

Diet Category	Fall	Winter
Seeds	64	60
Grasses	12	22
Berries	9	0
Bulbs	5	0
Unknown	5	4
Insects	3	1
Greens	2	12

TABLE 2. Frequency of occurrence (%) and dry weights (%) of major food items found in mountain quail crops (n =90) during fall (1994-96) and winter (1998-99) in the southwestern Cascade Mountains, Oregon (a = non-native species).

	Fall			Winter	
Taxon	Frequency	Weight	Taxon	Frequency	Weight
Insects	73	3	Miscellaneous greens	82	12
Lotus spp.	58	18	*Vicia hirsuta* (a)	50	36
Miscellaneous greens	26	2	*Caucalis microcarpa*	50	5
Festuca arundinacea (a)	25	9	Insects	48	1
Cynosurus echinatus (a)	25	3	*Arctostaphylos* spp.	32	1
Madia spp.	25	1	*Cynosurus echinatus* (a)	25	16
Rubus spp.	24	5	*Bromus* spp.	25	5
Vicea sativa	22	3	*Lotus* spp.	25	4
Ceanothus spp.	22	2	*Crataegus* spp.	18	2
Arctostaphylos spp.	22	2	*Trifolium* spp.	18	2
Medicago lupulina (a)	21	5	*Festuca arundinacea* (a)	11	1
Cytisus scoparius (a)	20	7	*Oryzopsis* spp.	7	1
Trifolium spp.	20	3	*Phalaris* spp.	7	1
Symphoricarpos spp.	20	2	*Triticum* spp. (a)	4	6
Unknown seeds	16	4			
Vicia hirsuta (a)	16	1			
Lathyrus spp	16	7			
Vicia villosa (a)	13	1			
Garrya fremontii	9	5			
Bulbs	8	5			
Lupinus spp.	8	2			
Berberis spp.	8	1			
Plagiobothrys spp.	4	4			

Crops collected in the winter contained parts from 37 plant taxa. Seeds were the most prominent items found in crops and constituted the greatest biomass of food contents (Table 1). The legume family was commonly used, primarily hairy vetch (*Vicia hirsuta*) (Table 2). Vetch was found in 15 of 29 (50%) of the crops and was 36% of the total dry weight. Deervetch appeared in 25% of the crops, but constituted <5% of the dry weight. California hedge-parsley (*Caucalis microcarpa*) was found in 14 of 29 (50%) crops and made up 5% of the dry weight. Manzanita occurred in 9 of 29 (32%) crops, but accounted for only 1% of the dry weight. Hawthorn (*Crataegus* spp.) was found in 5 of 29 (18%) of winter crops and was 2% of the dry weight. Tall fescue, dogtail's grass, and bromes (*Bromus* spp.) were the most common grasses eaten and constituted 22% of the total dry weight. Unidentified green foliage was found in 82% of the crops and accounted for 12% of the dry weight. Insects (ants, beetles, centipedes, grasshoppers, and millipedes) from five orders (*Hymenoptera*, *Coleoptera*, *Scolopendromorpha*, *Orthoptera*, and *Chordeumida*) were in 14 of 29 (48%) of the crops, but constituted only 1% of the dry weight.

Discussion

We confirmed that during fall and winter mountain quail in the southwest Oregon Cascades consumed a diverse range of food resources. For the combined seasons, mountain quail consumed items from 61plant genera and species. The bulk of quail diets was composed of a few seasonally abundant plants. In the winter when food resources were likely less abundant, they selected from a greater range of food items and consumed more green leafage. Legumes were especially important in fall and winter diets, and represented a substantial proportion of the plants that were consumed. Particularly prevalent in fall crops were species of deervetch. This genus (*Lotus* spp.) in the Cascade Range is composed of both introduced birdsfoot-trefoil (*Lotus corniculatus*) and native species, and is widely distributed in moist, disturbed sites (Richard Helliwell, Umpqua National Forest Botanist, personal communication).

In Madera, Tuolumne, and Tulare counties in the Sierra Nevada region, and Fresno county in the Great Central Valley region of California, 22% (by volume) of mountain quail crop contents collected during the summer and nearly 19% collected during the fall was Spanish clover (*L. americanus*) seeds (Gutiérrez 1977). Other frequently selected species during the fall in the southwestern Cascades were black medick, peavine, and vetches. Legumes, particularly clover, lupine (*Lupinus* spp), and vetches, were important food items in the diets of mountain quail collected in southeastern Washington (Yocum and Harris 1953) and California (Gutiérrez 1977). The importance of legumes in other quail diets has been noted (Gullion 1966, Shields and Duncan 1966, Landers and Johnson 1976, and Blakely et al. 1993), evidence that this plant family provides a considerable source of nutrition. Duke (1981) listed a protein content of 35% for desert lotus (*Lotus rigidus*), 33% for black medic and peavine, and 25-48% for vetches. We also found that blackberries, huckleberries (*Vaccinium* spp.), snowberries, and two grasses (tall fescue and dogtail's grass) were relatively important in fall diets. In southeastern Washington, berries from smooth sumac (*Rhus glabra*) constituted nearly 25% of the total dry weight in mountain quail crops collected during the fall (Yocum and Harris 1953). However, in western Idaho and Nevada, berries were not an important food during the fall (Ormiston 1966, Gutiérrez 1977). Grasses were not a significant fall food for mountain quail in Idaho and Washington (Yocum and Harris 1953, Ormiston 1966), but in two counties of California, grass leafage constituted 19% of the total volume of fall crops (Gutiérrez 1977). Despite appearing in 73% of fall crops collected in the western Cascades, insects were only 3% of the total volume. Insects were eaten in greater quantities during the summer in the Great Basin, but represented <15% of the food used by mountain quail in fall and winter (Gutiérrez and Delehanty 1999).

Mountain quail used more food items in the winter, but many fall foods were not used in the winter, or were consumed in lesser amounts. We found less deervetch in winter crops, and no black medic, lupine, or peavine. Hairy vetch, the only species of vetch consumed in the winter, accounted for 36% of the total volume of winter crops. Dogtail's grass was more heavily represented in winter crops, but fescue was found in lesser quantities. In comparison with the fall, green herbage occurred more frequently in winter crops and was found in greater quantities. Insects were selected less often during the winter and accounted for less of the total volume. Gutiérrez (1977) noted that in some areas of California, mountain quail shifted diets between fall and winter to take advantage of temporarily abundant foods. For example, he found that acorns were used heavily during the fall in Riverside and San Bernardino counties but figured much less prominently in winter diets. Compared to fall diets, leafage (*Erodium* spp. and Gramineae species) was found more extensively in winter crops, and mountain quail shifted from a fall diet composed largely of legumes (*Lotus* spp. and *Lupinus* spp.) to a winter diet composed prominently of ponderosa pine (*Pinus ponderosa*) and manzanita.

Mountain quail are closely associated with early successional vegetation, particularly shrub-dominated communities (Gutiérrez and Delehanty 1999). Many of the plants selected during the fall and winter are disturbance-related, introduced species, or native species typically found in disturbed sites (Richard Helliwell, Umpqua National Forest Botanist, personal communication). Black medic is a weedy exotic that thrives on highly disturbed sites and tall fescue is an introduced grass common along logging roads in the Cascade Range. Tall fescue is a common, weedy grass found along roadsides and disturbed openings. Hairy vetch is an introduced European legume that is widely distributed along trails and ditches, and Scot's broom is a noxious weed often found in disturbed ground along roadsides (Hitchcock and Cronquist 1973). Mountain quail in the southwest Cascades of Oregon are opportunistic foragers that seasonally and regionally adjust their diets.

Acknowledgements

We greatly appreciated the collection efforts of members from the Oregon Hunter's Association, Oregon Department of Fish and Wildlife, and graduate students from Oregon State University. We thank M. Black and S. Denney from the Oregon Department of Fish and Wildlife and T. Cowin for technical assistance. We thank Oregon State University's Seed Laboratory for their help in identifying seeds. We also extend our appreciation to G. Miller and J. Rammakka from the Bureau of Land Management for funding part of this

project. We thank D. Edge and R. Lemon for reviewing earlier drafts of this manuscript and suggesting improvements. We thank T. Heekin and R. Gutiérrez for their reviews and excellent comments. Publication of this paper is supported in part, by the Thomas G. Scott Publication Fund. This manuscript is number 11831 of the Oregon Agricultural Experiment Station.

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Received 3 October 2001
Accepted for publication 31 January 2002

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Book Reviews

101 Common Mosses, Liverworts & Lichens of the Olympic Peninsula

Martin Hutten, Karen Hutten, and Andrea Woodward. 2001. Cooperative publication of USGS, Canon USA, Inc., National Park Foundation, Olympic National Park, and the Northwest Interpretive Association. 109 pages. ISBN 016-066471-3. Softcover, $8.95. Copies of the booklet can be obtained from the Seattle (206-553-4270) or Portland (503-221-6217) Government Printing Office.

The cryptogams feature in people's visual impressions of habitats in the Pacific Northwest, particularly those regions commonly known as the rain forest, but few people realize it because popular guides to these organisms are not available. Prior to this publication there has been little in the way of a comprehensive, informative, yet simple introduction to these organisms. The guide is immediately aimed at introducing the Olympic National Park visitor to this group of non-vascular cryptogamic "plants." It meets this goal well and should also prove useful to a larger audience and in a wider geographic range.

The guide is pocket-sized (13 x 15 cm), spiral bound and includes introductory material followed by 101 pages, each detailing a common or conspicuous species. The introduction includes just enough material to get the user started and additionally provides information on general ecological and economic importances. On each species page, beautiful, color photographs provide the means to identify the focus species while occasional inset photos provide additional details of microscopic structures, habits or similar species. On the bottom of each page, one or two similar species are briefly discussed, so that the guide can actually be used to differentiate about 240 species. The focus species are grouped through the guide among one of six substrate types (Forest Floor, Logs, Conifer, Hardwood, Streamside, Rock). Within each substrate group the mosses come first, then the liverworts, and finally the lichens. Within each of these taxonomic groups, the species are listed alphabetically. Only a few, more conspicuous, crustose lichens are included. The expected range of elevation for each main species is indicated by a scale on the margin of each page. A brief glossary (technical terminology is correctly kept to a minimum) and index follow.

The format may be most appropriate for the audience (I will be interested to see how it works with my field seminar students), although the overall organization by substrate type may be confusing to the first-time user. There is considerable crossover of species between substrates. Quickly finding the reference to the lichen *Cladonia bellidiflora*, which one has found on a forest log (a common habitat for this species) will be more difficult since one must search the Conifer section. Likewise, to find *Ptilidium californicum*, which most often is seen on the bases of conifer trunks at mid elevations, one must search the Log category. For some reason, *Thamnolia vermicularis*, which only grows in exposed locations (alpine rock and soil) where there are few if any trees, is included in the Forest Floor category. I wish the taxonomic groups were kept together and that, within them, species were arranged by overall appearance (habit for the mosses and liverworts, and growth form for the lichens) and size. The ranges in substrates for each species could then be indicated by a selection of icons. Nevertheless, the arrangement should allow the user eventually to find most species they first run across.

The information about each species is useful, interesting, and at a level and amount adequate for a guide of this sort. As far as I can see, aside from some of my quibbles over substrate assignment indicated above, this information is correct. The photographs do not include scales, so that it is more difficult to get feeling of size without reading text. The coverage is quite complete, particularly of the lowland species, considering the size of this resource. However, among the lichens, a *Melanelia* species, common everywhere, and *Cavernularia lophyrea*, which is common at some coastal locations, are not included. High elevation species are underrepresented. The following lichen genera that include conspicuous and

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distinctive species at high elevations were not detailed with species from those locations: *Cetraria*, *Solorina*, *Peltigera*, and *Hypogymnia*.

The minor drawbacks should not deter beginning students, field naturalists, and interested visitors to our natural habitats from purchasing and using this guide. Although focused on the Olympic peninsula, it should be useful throughout the western side of Washington and down into the coastal range in Oregon.

—Fred M. Rhoades
Research Associate
Biology Department
Western Washington University
Bellingham, WA 98225

The Restless Northwest: A Geological Story

Hill Williams, 2002, Washington State University Press, Pullman, Washington, 176 Pages. ISBN 0-87422-250-8. Paperback, $19.95

The Restless Northwest is a very readable, short book with an easy flowing style. Compact enough to fit into a jacket pocket, it will make a fine reference for travelers throughout the Northwest who want to learn about the billion-year history of the region.

Despite earthquakes and volcanic eruptions, most of us think of our surroundings as stable and enduring. *The Restless Northwest* describes that indeed much of North America has remained stable after undergoing a series of convulsions that assembled the continent from about 3.5 to 1 billion years ago. And for the last 500 million years, nothing much happened to the middle of the continent except the accumulation of sediment, thickest along the edges of the continent. But all throughout geologic time, the continents were in motion. About 400 million years ago, the Atlantic Ocean closed, crushing the rocks along the eastern seaboard to create the Appalachian Mountains and connect all of the continents into a super-continent called Pangaea. Then, about 200 million years ago, Pangaea broke up and its parts drifted over the surface of the earth. One of the largest breaks occurred between Europe/Africa and the Americas, resulting in the reborn Atlantic Ocean.

Williams explains that the land beneath Washington and Oregon is a relatively recent addition to the North American Continent. About a billion years ago, a fragment split off from North America and drifted off into the west, leaving the edge of the continent roughly along the Idaho-Montana border. But as North America moved westward away from Europe and Africa about 200 million years ago, it forced the Pacific Ocean floor to slide, or subduct, beneath the continent. The continent scraped off old volcanic rock and bits and pieces of continental crust riding on the oceanic plate. These scraped-off fragments form the crust of Washington and Oregon. Continued subduction resulted in the chain of volcanoes that form the Cascade crest.

Hill Williams, a former *Seattle Times* science writer, draws on the collected experience of many local geologists to tell the story of events that shaped our landscape. The first four chapters in this book briefly outline the early history. The discovery of large-scale continental movements is fascinating, and Williams gives a sense of the joy and awe of this relatively recent discovery in the second chapter. The next chapter provides a detailed look at the edge of the continent more than 500 million years ago when the large fragment of crust that now forms the Pacific edge of the Northwest separated from the rest of North America. Thick Belt and Windermere sediments collected along the new margin, now well exposed in Glacier National Park.

Chapter 4 sets the stage for the later history of the Northwest by describing the assembly and breakup of the super-continent Pangaea. The Atlantic Ocean reopened about 200 million years ago and North America has been moving west ever since, pushing against the Pacific oceanic plate that still slides beneath the continental margin.

The stage is now set for the building of the Northwest. Chapters 5 and 6 describe the building of the crust that lies beneath Washington, Oregon, and British Columbia. This is a complicated story and the reader may be forgiven for skimming over these chapters. As the Pacific plate moved eastward, it carried volcanoes, sediments, and fragments of disrupted continents. When the plate slid under North America, these fragments were scraped off and welded to the continent. Williams describes the arrival of several of these terranes, some of which contain fossils that show the rocks were from southeast Asia. The movement of the plates against one another was at an oblique angle, so that some of the terranes have since traveled north along the coast. Wrangellia, the terrane that stretches from Alaska to Vancouver Island and beyond, is thought to have docked with North America at the latitude of Mexico and subsequently moved more than a thousand miles northwards. No wonder geologists are confused when examining Northwest rocks!

About 50 million years ago the terranes settled into their current locations, and local geology becomes more understandable. The coastline still crossed lower Puget Sound to the Oregon-Idaho border, whence it headed south. Northward movement of one of the Pacific Plates—the Kula Plate

that disappeared beneath Alaska about 40-50 million years ago—tore at the coastal region, leaving a legacy of north-south faults in northern Washington. Much of what is now Washington and Oregon lay beneath or at sea level in a broad basin, called the Columbia Basin—though it bears no relation to the present Columbia Plateau. Sediments poured into the basin, and volcanoes erupted along its margin, together forming the foundation of much of our land. Parts of the basin were swampy and accumulated plant debris that later was compressed to create the coal fields of western Washington.

Cascade andesite volcanoes that had been active for about 30 million years ceased about 17 million years ago, and the crust behind them began to stretch and crack. Great volumes of a different kind of volcanic rock—basalt—erupted from fissures in the crust in eastern Washington and Oregon and flooded the Columbia basin as far as the now gently rising Cascade Range. They even flowed nearly to the present coastline between present-day Washington and Oregon, in what is now the Columbia River valley. The last of these magnificent lava flows erupted about 12 million years ago. The reader will have to skip to Chapter 9 for a full discussion of the Columbia River basalts. I wondered why this break in the action is described later.

This tale of volcanoes and swampy basins is well described by Williams, though the reader can be overwhelmed by the numerous changes in the interaction between the subducting Pacific plates—first Kula, later Farallon—with the continent that was shedding sediments from the land. But blame the geology, not the author! When the Columbia River basalts were erupting, the Cascades were still only a range of low hills. The Cascade volcanoes burst back into life when the movement of the Farallon plate changed about 10 million years ago to thrust more directly against the coastline. The low hills rose rapidly and large volcanoes tipped the ranges, as they continue to do today. Some of the volcanoes exploded spectacularly. Mount Mazama in Oregon erupted about 6,900 years ago to create Crater Lake; Glacier Peak sent up a plume of ash 12,000 years ago that dwarfs the 1980 Mount St. Helens eruption; and though not mentioned by Williams, Mount Baker erupted about 1 million years ago in a most spectacular fashion.

The Ice Ages, and in particular the Lake Missoula floods that devastated eastern Washington, are covered in chapters 10 and 11. Glaciers carved deeply into our landscape as far south as Olympia in Puget Sound, and to south of the Columbia River in northeastern Washington. Clear maps and excellent descriptions show the extent and action of the Lake Missoula floods. These floods resulted from the failure of an ice dam in Idaho that had created Lake Missoula to the east. The landscape is now familiar to the reader and this section is easy to follow.

The final chapter warns us of the dangers ahead. We may be aware of earthquake and volcanic hazards, but Williams conveys a compelling sense of urgency. We are constantly discovering more about events of the past tens of thousands of years, including a great earthquake in 1700 that produced a tsunami in Japan. Alki Point in Seattle rose nearly 20 feet just 1,000 years ago, resulting in a tsunami that must have devastated Puget Sound. Numerous mudflows have poured down repeatedly from Mount Rainier; the cities of Auburn and Puyallup, south of Seattle, are built on these mudflows.

The Restless Northwest will not compete with the *Roadside Geology* series that is geared to the motorist, but it provides a thoughtful companion to those who wish to understand how our landscape evolved.

—Jim Talbot
Department of Geology
Western Washington University
Bellingham WA 98225-9080

NORTHWEST SCIENCE

Information for Authors

Purpose and Scope

The Northwest Scientific Association represents the natural and social sciences in the Pacific Northwest. The pages of *Northwest Science* are open to original and fundamental research in the basic and applied natural and social sciences. All submissions are refereed, usually by two reviewers and an Associate Editor. Papers are welcome from authors outside of the Pacific Northwest.

Web Site Information

Authors should visit the Northwest Scientific Association web site to obtain the most recent version of Information for Authors. The web site address is: www.vetmed.wsu.edu/org_NWS/NWSci_Home.htm

Articles

Articles present the results of new and original research, and generally are 6–20 journal pages long. Authors must contact the Editor in advance before submitting longer papers. Authors are encouraged to use line numbering for the original submission, which will help speed up the review process.

Notes

The purpose of Notes is to publish papers typically less than five journal pages long. Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for Notes, but all will be peer-reviewed and must be scientifically creditable. Authors may contact the Editor about the suitability of manuscripts to be published as Notes.

Northwest Science Forum

This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

Manuscripts

General Instructions

Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point Times New Roman font, on 8.5" x 11" paper, double-spaced throughout (including Abstract, Acknowledgements, Literature Cited, Tables, and Figure captions). Allow one-inch margins around the page. The format and style of manuscripts should conform to general usage in recent issues, and should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgements)
- Literature Cited
- Footnotes
- Tables
- Figure Captions
- Figures

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In that situation, lowercase letters will be used. Do not hyphenate words at the ends of lines. Words to be italicized will be typed in italic rather than underlined.

Title Page

The first page of the manuscript should contain:

- Author name(s)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running footer (for right-hand pages)
- Total number of tables and figures
- List the name, full address, telephone number, fax number, and e-mail address of the author to whom correspondence should be sent. Use a footnote to indicate a corresponding author other than the senior author. For example: "[1]Author to whom correspondence should be addressed."

Abstract

The second page of the manuscript contains the Abstract. Authors are strongly encouraged to give the abstract proper attention. The abstract briefly summarizes the study, so that it is quickly accessible to the general readership of the journal. The abstract must be written in complete sentences and may not exceed 250 words. Because of the diverse disciplines and readership served by the journal, the abstract should include the following three parts: 1) a statement of the purpose of the study, indicating the reasons behind its undertaking; 2) a statement describing the experimental design or approach and a summary of the results; 3) a summarizing sentence or two regarding the larger significance of the research.

Text

Start the text on the third page, and use continuous pagination. Do not start new sections on new pages.

Literature citations within the text should contain the author's name and year of publication, using formats A and B. Multiple citations of authors within the same parentheses will be listed in chronological order.

- Format A:

...studied by Jones (1998)...

...studied by Smith and Brown (1999)...

...studied by Smith et al. (2000)...(if more than two authors in a citation)

- Format B:

...was previously investigated (Smith 1991, Jones 1995, Harris 2000)

...results of other investigations (Smith 1991, 1995; Jones 1993; Brown 1999)

Numbers from one to nine will be spelled out, while Arabic numerals will be used for numbers 10 and larger. Exceptions to this convention are: 1) a series of mixed numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 5 g, 0.7 mm, 3 m^2). Arabic numerals will also be used for dates, times, page numbers, and percentages.

Authors are requested to use the International System of Units (SI). Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1998). Use leading zeroes with all numbers <1 (e.g., 0.12), including probability values with "*P*" capitalized and italicized (e.g., $P \leq 0.05$). Please note these examples of other conventions followed by *Northwest Science*: 20th Century, 3rd Edition, Douglas-fir, dbh, sec, min, hr, day (or d), wk, mo, yr. Please do not use the construction "and/or" because "or" invariably will suffice.

On first mention in the text, a species should be designated by common name followed by systematic binomial (italicized). If a common name is available, systematic binomials are unnecessary, and are not recommended, in the Title and Abstract. Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." In general, authors should follow conventions for their disciplines (e.g., botany, ornithology). Consult with the Council of Biology Editors *CBE Style Manual*, 4th ed., for general information on manuscript preparation.

Personal Communications

These should be kept to an absolute minimum, because they do not meet the requirements for first disclosure as defined by the Council of Biology Editors. If used, the full name and affiliation of the person being quoted is required. *Personal communications are cited in the text,* not in Literature Cited. For example:

... (David L. Peterson, University of Washington, personal communication).

Literature Cited

Only the *first letter* of the *first word* of journal articles, technical reports, theses, symposia papers, and technical bulletins are capitalized. First letters of *major words* in book titles are capitalized. All authors and editors of a title will be listed in the bibliographic citation. Use "et al." only in the body of the text, never in the Literature Cited section.

Citations should be double-spaced and listed in alphabetical order at the end of the article. *Note that the names of all sources are spelled out.* The only exceptions are the commonly used abbreviations USDA, USDI, EPA, and USA. The abbreviations USDA and USDI must be followed by the name of the agency (e.g., USDA Forest Service; USDI Bureau of Land Management).

Double-check literature to ensure that citations in the text and in Literature Cited agree. On one submitted copy, indicate by green check marks on each citation in the text and each citation in Literature Cited that the references have been double-checked.

The general format for citations is:

- Last name, initials of the first name and middle name, then switch to initials followed by the last name for subsequent authors.
- Use a space between initials and names.
- Short bar. Beginning with the Fall 2001 issue, *Northwest Science* will no longer use a short bar for repeated entries by the same author.
- Issue numbers are unnecessary.
- Double-check each citation to ensure that it conforms to the *Northwest Science* format.

Typical examples of *Northwest Science* format conventions for Literature Cited are as follows:

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus*. Journal of Mammalogy 51:310-326.

Broadbooks, H. E. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus*. American Midland Naturalist 83:472-488.

Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Edmunds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York. *(number of pages unnecessary)*

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393 *In* H. Barnes (editor), Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

Theses, dissertations, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary ponds in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. Ph.D. Dissertation, University of Utah, Salt Lake City, Utah.

Dunwiddie, P. W. *In Press*. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science. *(if the publication date is unknown or uncertain)*

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: *(in press). (if the publication date is known and certain).*

Technical bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Online (web) references

USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

Unpublished Reports

Unpublished reports often contain useful data that contribute to the development of the study being

reported. Even though they do not meet the criteria for first disclosure, if they have a date, author, and a location where the report is on file, so that interested readers can obtain a copy of the report, they may be listed in Literature Cited so that the text reads more smoothly. If the date is unknown, treat the report as a personal communication and cite it in the text. If the location is unknown, do not use the report.

Kraft, G. F. 1967. Annual report on the status of Lake Whatcom. Unpublished report on file at Western Washington University, Bellingham, Washington.

Footnotes

Footnotes to the text are discouraged. In most cases, the potential footnote information can easily be incorporated in the text. If footnotes are unavoidable, they must be numbered consecutively and clearly indicated in the text.

Tables

All tables must be cited in the text, but typed and double-spaced on separate pages. Set up tables using tab stops; do not use auto-formatted tables. Note that the word "Table" is in all caps at the beginning of the TABLE caption, but in lower case in the text. When submitting tables electronically, *they should be presented in the simplest tabular format possible*, and placed after the body of the manuscript. Use letters as superscripts to indicate statistical differences among values being compared (numbers with different letters indicate significant differences at $P \leq 0.05$) Footnotes to tables are numbered consecutively with each table treated as a separate entity (i.e., the first footnote on each table should be 1).

Figures

All figures must be cited in the text. To achieve highest quality reproductions, it is preferable for the printer to work directly from photographs or original drawings. Thus, original artwork or 5" x 7" (or larger) black & white glossy prints of photographs must be submitted for reproduction. Mount photos on lettering board to protect them from damage. Artwork and lettering should be large enough (but not overly large) to provide clarity after a 50% reduction in size for printing. *The author's name, figure number, and indication of "top" should be penciled on the back of each illustration.* Illustrations of study areas should include a small inset that locates the study area in the state or province. Provide a scale for distance on map illustrations. Captions for illustrations should be typed as a group and placed on a separate page. The words Figure and Table will be spelled out in the body of the text, and capitalized as follows:

- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photos, and other illustrative material cannot be returned to the author.

Editing

The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

Submission of Final Copy

Manuscripts accepted for publication must be submitted in electronic copy and hard copy. Authors will receive instructions from the Editor regarding this procedure.

Publication Agreement

Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

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One set of page proofs will be sent to the corresponding author for correction shortly before publication. **Proofs must be returned to the Editor within three days of receipt—preferably by express mail.** Authors must inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs. Allow 8 weeks for delivery after the journal issue carrying the article appears.

Page Charges

Page charges are currently $65 per printed page for members of the Northwest Scientific Association, and $80 for non-members. Authors wishing to become members may contact the Treasurer.

You must submit some form of payment with the order form and the proofs. It is not sufficient to request an invoice from the Association. Institutional checks, personal checks, money orders, and credit card orders are acceptable and should accompany the page proofs. **If an institutional purchase order is being used for payment, then the purchase order must accompany the page proofs.**

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WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

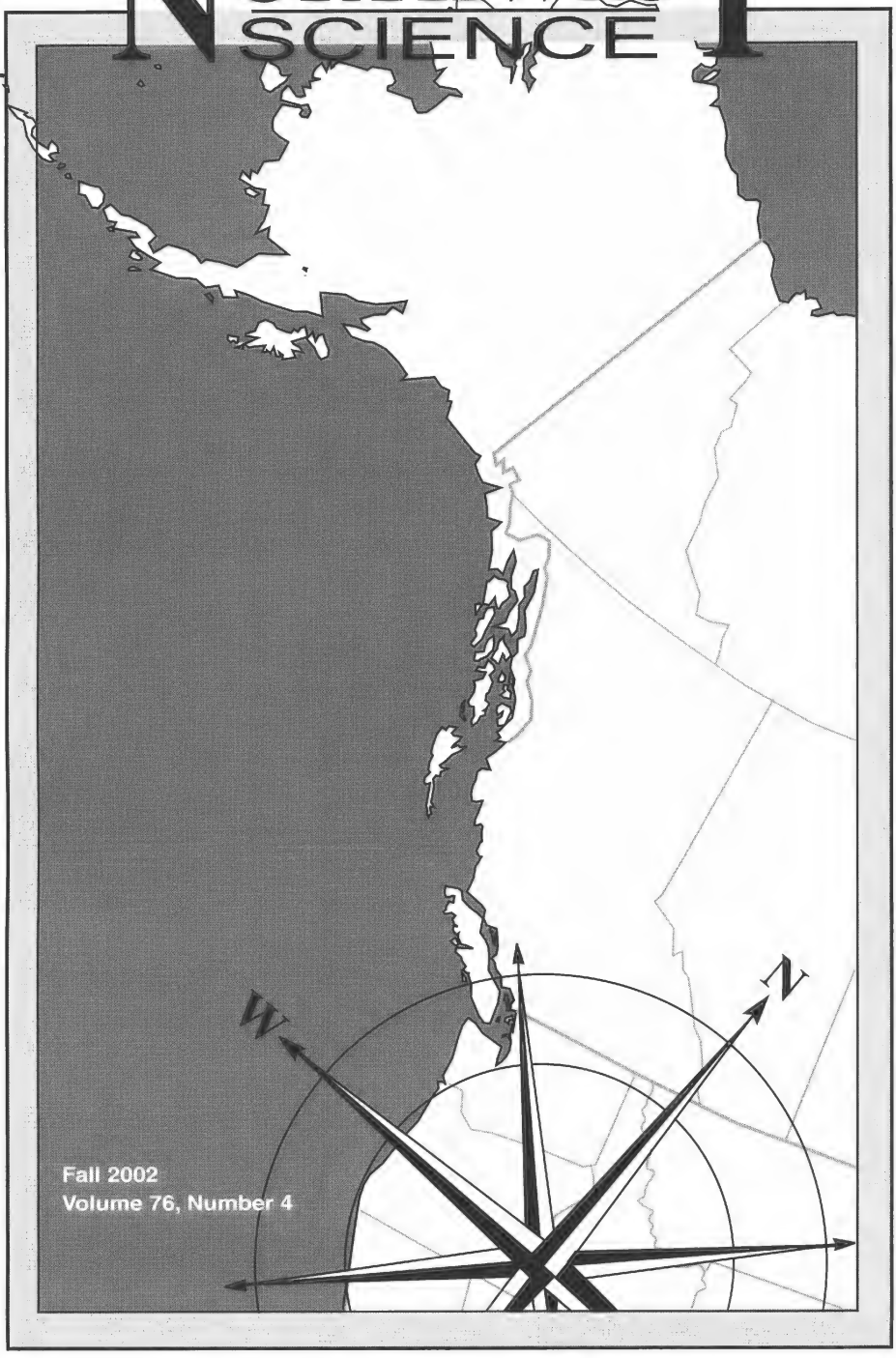
Northwest Science

Quarterly Publication of the Northwest Scientific Association

Presorted Standard
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*

NORTHWEST SCIENCE



Fall 2002
Volume 76, Number 4

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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The Northwest Scientific Association is a 501-C(3) tax status organization.

Editor of *Northwest Science*

Rich Fonda
Biology Department
Western Washington University
Bellingham, Washington 98225
Telephone: 360-650-6599
Fax: 360-650-3148
Internet: fonda@biol.wwu.edu

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Department of Biology
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Department of Biology
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Fall 2002 Volume 76, Number 4

NORTHWEST SCIENCE

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ISSN #0029-344X

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Information for Authors

Announcements

2003 Annual Meeting, Forks, Washington, 26-29 March

The 76th Annual Meeting of the Northwest Scientific Association will occur at the Olympic Natural Resource Center in Forks, Washington, from Wednesday, 26 March through Saturday, 29 March, 2003. The meeting will be held in conjunction with the Northwest Lichenologists, Oregon white oak working group, USDI National Park Service, USDA National Forest Service, the Washington Department of Natural Resources, and the University of Washington. Field trips are planned for dates before and after the meeting. The major symposium will be on sustainable forestry. Proposed concurrent sessions, symposia, and workshops are scheduled, and both oral presentations and poster presentations are planned.

- Botany session
- Ecology session
- Marine/Aquatic Biology session
- Lichen session
- Zoology session
- Lichen identification workshop
- National vegetation classification discussion group
- Natural areas workshop
- Oregon white oak workshop

Individuals interested in helping to organize sessions or workshops should contact Dan Stephens, Wenatchee Valley College, 1300 Fifth Street, Wenatchee, WA 98801. Phone: 509-664-2503. FAX: 509-664-2538. E-mail: dstephens@wvcmail.ctc.edu.

Registration and accommodation information is available on the NWSA web site, listed on the inside front cover of this issue.

Northwest Scientific Association 2003 Student Research Grant Competition

The Northwest Scientific Association annually awards grants of up to $1000 to support student research in the pure and applied sciences. Applicants must be student members of NWSA (see inside front cover of *Northwest Science* for membership application information). Monies can only be used to support travel, equipment, and supplies for student research (proposals requesting salary support will not be considered).

Proposals should include (in the following order): 1) a cover page that provides the project title, name and address of the student applicant (including phone number and e-mail address), name of the major professor or advisor, and the dollar amount requested; 2) the body of the proposal, which provides an introduction (including the research question(s), objective(s) and significance), the literature background, the project methods (including experimental design, methodologies, appropriate statistical analyses, and timeline), and expected results; 3) literature cited; 4) supplementary tables and figures; and 5) an itemized budget ($1000 maximum). The body of the proposal may not exceed four pages of double spaced text in 12-pt font with one inch margins (excluding title page, literature cited, supplementary tables and figures, and budget).

Four copies of the proposal must be received on or before 1 February 2003, and sent by surface mail to:

Dr. Karl Lillquist
Geography and Land Studies Department
Central Washington University
Ellensburg, WA 98926

Grant winners will be announced at the 2002 NWSA annual meeting in Forks, Washington in March 2003. Grant recipients are required to present the results of their research at a future Northwest Scientific Association annual meeting. NWSA will waive page charges if grant recipients choose to publish their research in *Northwest Science* within four years of accepting their grant. Questions concerning grant application procedures should be directed to Dr. Karl Lillquist via e-mail (lillquis@cwu.edu).

Call for Nominations

Nominations are invited for Honorary Life Member and Outstanding Scientist awards for the year 2003. Honorary Life Memberships are awarded to individuals who have contributed to the continuing success of the Northwest Science Association with enthusiasm and devotion. Outstanding Scientists are individuals who have made significant contributions to our understanding of basic or applied scientific issues relevant to northwestern North America. Nominations for both awards should be forwarded to Paul Verrell (E-mail: verrell@wsu.edu), no later than 1 January 2003.

Wildlife Biology Associate Editor

The new Associate Editor for Wildlife Biology is Dr. William Gaines, a Wildlife Ecologist for the Okanogan-Wenatchee National Forests who recently received his Ph.D. from the University of Washington in Wildlife Science. Bill has been a member of the Northwest Scientific Association since 1986 and a member of the Wildlife Society since 1989. His current interests include research and conservation of large carnivores, and monitoring the effects of forest management on wildlife habitat and populations.

Dr. Patricia Heglund stepped down as Associate Editor for Wildlife Biology in May. When Pat began her four-year tenure as associate editor, she was a wildlife biologist with the Potlatch Corporation in Lewiston, Idaho. She assumed the position of Regional Refuge Biologist for the Fish and Wildlife Service in Anchorage, Alaska in 2000, and recently moved to LaCrosse, Wisconsine where she became Branch Chief, Terrestrial Ecology at the Upper Midwest Science Center. She was responsible for guiding 61 manuscripts through the review process. She coupled this responsibility with her research into wildlife habitat relationships, particularly with species-environment relationship models. We appreciate your hard work and dedication, Pat. Thanks!

Zoology Associate Editor

The new Associate Editor for Zoology is June R. P. Ross, Professor in the Department of Biology, Western Washington University. Her degrees are B.Sc., Ph.D. and D.Sc. from the University of Sydney (Australia) and she has been on the faculty at Western for a number of years. She brings expertise in general zoology, marine invertebrates, oceanography, and evolution, courses she has taught at Western for many years. She has published more than 140 books and articles that range from a textbook on insects to books and articles on marine invertebrates and bryozoology, biogeography, and the interactions of faunal dispersal and sea level fluctuations. No stranger to editing, she

has edited a number of volumes of various scientific symposia and has served as an associate editor.

The previous Associate Editor for Zoology, Richard Forbes, of Portland State University, died shortly after heart surgery in July 2002. Dick became Associate Editor in 1994. During his 9-year tenure for the journal, he was responsible for guiding 30 manuscripts through the review process. He did his job with considerable aplomb and diplomacy, and his contribution will be sorely missed.

Ronald J. Taylor Research Natural Area

On April 11, 2002, the USDA Forest Service formally designated the Ronald J. Taylor Research Natural Area. This Area is located on the northwest side of Mt. Baker, on the Mt. Baker-Snoqualmie National Forest, in Whatcom County, Washington. This 1089.40 hectare Research Natural Area centers on Chowder Ridge, but also includes portions of Skyline Divide, Cougar Divide, and adjacent streams. Elevations range from 1360 m to 2320 m.

This Research Natural Area was named after Dr. Ronald J. Taylor to recognize his many years of research and teaching on Chowder Ridge. During his career at Western Washington University, Ron was a staunch advocate of the Northwest Scientific Association, serving as a member of the Board of Trustees for many years and as President in 1978-1979.

Research Natural Areas are designated in perpetuity on lands that illustrate or typify important vegetation types, as well as other plant communities that have special or unique characteristics of scientific interest and importance. They are managed to maintain natural conditions insofar as possible, with research and education identified as the primary purpose

The Ronald J. Taylor RNA was established because of its unique alpine environment and vegetation. Chowder Ridge contains the largest area of continuous alpine vegetation in the western North Cascades. Twelve plant community types have been described. Vascular plants include those common to the western North Cascades, as well as species more common to the Rocky Mountains. Two hundred lichen species and 74 species of bryophytes have been documented, many of which are rare to Washington State. Landforms characteristically associated with the alpine zone are present, such as frost heaving, rock stripes, vegetation stripes, solifluction lobes, and fell-fields. Conspicuous wildlife species include mountain goats, with an occasional blacktail deer, cougar, coyote, and wolverine.

Jay E. Anderson Endowment

Jay E. Anderson, Professor Emeritus at Idaho State University, passed away 4 July 2002. He was the recipient of the Northwest Scientific Association's 2001Outstanding Scientist Award. The Ecological Society of America has established the Jay E. Anderson Endowment that will honor Jay's life and memory by sponsoring projects and programs that explore and advance his concerns for and love of the ecosystems of the west and Pacific Northwest. The Endowment will be action oriented and may sponsor activities of many kinds, including, for example, symposia; workshops or discussions with policy makers, industry groups, NGOs, land users, or owners; policy for a or briefings in Washington, D.C., or in the west; educational programs; special features in tecyhnical journals or publications for non-scientists, such as Issues in Ecology. The Endowment's activities will be selected by an ESA committee, with rotating memberhip, which can originate ideas for activities and can review and select from suggestions or proposals submitted by others. Send tax-deductible contributions as checks payable to "ESA – Jay E. Anderson Endowment" to Ecological Society of America, 1707 H Street NW, Suite 400, Washington, DC 20006.

Reviewers Needed: A Note from the Editor

All articles and notes published in *Northwest Science* are peer-reviewed. This process of bringing a manuscript to publication is fairly simple. Submitted manuscripts are sent to Associate Editors, who contact potential reviewers. When the reviews are returned, the Associate Editors summarize those reviews, add their own comments, and return them to the Editor who sends them on to the authors. This process depends on the cooperation of all of us in the scientific community, because both the strengths and weaknesses of the system are centered on reviewers. The high quality of papers published in *Northwest Science* is maintained by careful reviews. Finding competent reviewers, however, is a challenge for the Associate Editors. We all like to publish papers, but we also need to be willing to serve as reviewers for our colleagues so that their manuscripts get published, too.

To help the Associate Editors in their search for reviewers, I have created the form below. If you are willing to be a reviewer, please recreate the form and email it to the Editor at fonda@biol.wwu.edu. Please check the list of Associate Editors in the masthead, and indicate those broad subject areas in which you feel competent to serve as a reviewer. Also, indicate your expertise and the specific topics with which you are most comfortable.

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Won Shic Hong, Department of Biology, University of Great Falls, Great Falls, MT 59405-4934 Email: whong@ugf.edu

A Key to the Hepaticae of Montana

Abstract

A key emphasizing vegetative characters is provided for 132 species and 3 subspecies in 45 genera and 26 families of liverworts recorded from Montana. A list of synonyms is provided.

Introduction

The earliest paper of liverworts of Montana was published by Jones (1910). After his publication a number of authors added species to the hepatic flora of Montana, including Haynes (1910), Clark and Frye (1928, 1931, 1937), Hong (1967, 1968a, 1968b, 1970, 1971, 1972, 1975, 1977) and Hermann (1969). Also scattered distributional information was presented by Frye and Clark (1937-1947) and Schuster (1966, 1969, 1974, 1980, 1992a, 1992b).

A key to the liverworts of Montana has never been available and this study is intended to fill that gap (Hong et al. 1998). It emphasizes mainly vegetative characters to facilitate the identification of sterile material. In all, 132 species and 3 subspecies in 45 genera are included in the key. Two or more species of a genus are separately treated in a key to the species. A list of names previously recorded from Montana, which are now considered synonyms is provided. The nomenclature follows Grolle and Long (2000) and Stotler and Crandall-Stotler (1977).

Key to the Hepaticae of Montana

I. Plant body a thallus (somewhat leafy in *Fossombronia*) ..... Key A
I. Plants with leaves ..... Key B

Key A. General Key to Thalloid Liverworts (Metzgeriales and Marchantiales)

1. Thallus with internal differentiation; rhizoids smooth and tuberculate ..... 2 (Marchantiales)
1. Thallus without internal differentiation; rhizoids smooth only ..... 11(Metzgeriales)
2. Plants small, thalli 0.3-3.0 mm wide; sporophyte embedded in thallus; aquatic or on wet mud 3
2. Plants large, thalli 5.0-12 mm wide; sporophyte with very short foot and seta on thallus; terrestrial 4
3. Thallus linear, forked, branching; ventral scales absent ..... Key 2: *Riccia*
3. Thallus heart-shaped, forming rosettes on the surface of water; reddish-purple ventral scales present ..... *Ricciocarpos natans* (L.) Corda
4. Female receptacle from dorsal surface of thallus; radial walls around the pores thickened; star-shaped pores distinct ..... *Athalamia hyalina* (Sommerf.) S.Hatt.
4. Female receptacle from an apical notch of thallus; radial walls around the pores thin; star-like pores indistinct 5
5. Thallus with conspicuous gemmae cups on dorsal surface (usually) 6
5. Thallus without gemmae cups on dorsal surface 7
6. Gemmae-cups cup-shaped, with frilled margins ..... *Marchantia polymorpha* L.
6. Gemmae-cups semilunar with entire margins ..... *Lunularia cruciata* (L.) Dumort
7. Thallus with diamond-shaped markings 8
7. Thallus lacking diamond-shaped markings 9
8. Diamond-shaped markings distinct; midrib not obvious ..... *Conocephalum conicum* (L.) Underw.

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8. Diamond-shaped markings visible only with lens; midrib prominent below ..... *Preissia quadrata* (Scop.) Nees
9. Pseudoperianth (perianth-like sheath outside calyptra) present ..... Key 1: *Asterella*
9. Pseudoperianth absent 10
10. Polyoicous; carpocephalum (archegoniophore) unlobed; radial rows of 2-3 cells around pores ..... *Mannia fragrans* (Balbis) Frye & L. Clark
10. Monoicous; carpocephalum lobed; radial rows of 4-5 cells around pores ..... *Reboulia hemisphaerica* (L.) Raddi.
11. Thallus clearly differentiated into a midrib and unistratose wings 12
11. Thallus undifferentiated into a midrib and unistratose wings 13
12. Hair covering only one (ventral) side of thallus ..... *Metzgeria conjugata* Lindb.
12. Hair densely covering both sides of thallus ..... *Apometzgeria pubescens* (Schrank.) Kuwah.
13. Thallus margins uniformly lobed; black spot (*Nostoc*-cavities) present at base of lobes ..... *Blasia pusilla* L.
13. Thallus margins entire, black spot absent 14
14. Rhizoids purple to violet ..... *Fossombronia foveolata* Lindb.
14. Rhizoids colorless or brownish 15
15. Thallus flat to undulate; gametangia and sporophyte on dorsal thallus surface ..... Key 4: *Pellia*
15. Thallus pinnate or palmate; gametangia and sporophyte on short lateral branches 16
16. Thallus large (ca. 3-7 mm wide); greasy in appearance; oil-bodies numerous ..... *Aneura pinguis* (L.) Dumort.
16. Thallus small (ca. 0.3-2.5 mm wide); not greasy in appearance; oil-bodies solitary or absent (in *R. latifrons*) ..... Key 3: *Riccardia*

Key 1: *Asterella* P. Beauv.

1. Dorsal air chambers of thalli not divided by supplementary partitions; dorsal epidermis of thalli with thin walls ..... *A. gracilis* (F. Weber) Underw.
1. Dorsal air chambers of thalli subdivided by supplementary partitions; dorsal epidermis of thalli with thickened walls 2
2. Margins of thallus undulate when dry; ventral scales purple ..... *A. lindenbergiana* (Corda ex Nees) Lindb.
2. Margins of thallus strongly incurved when dry; ventral scales white ..... *A. saccata* (Wahlenb.) A.Evans

Key 2: *Riccia* L.

1. Absence of air chambers in transverse-section of thallus ..... *R. sorocarpa* Bisch.
1. Presence of air chambers in transverse-section of thallus 2
2. Thallus segments long and narrow; aquatic ..... *R. fluitans* L.
2. Thallus forming rosettes; terrestrial 3
3. Monoicous; thallus margin reddish-purple; spores areolate on external face ..... *R. cavernosa* Hoffm.
3. Dioicous; thallus margin purplish; spores ridged ..... *R. frostii* Austin

Key 3: *Riccardia* Gray

1. Thallus regularly 3-pinnately branched; thallus with a crenulate, transparent unistratose border, 2 cells wide ..... *R. multifida* (L.) Gray
1. Thallus palmately or irregularly branched; thallus lacking a transparent unistratose border 2
2. Autoicous; thallus larger (0.5-2.0 mm wide), yellow-green; branching irregular- palmate; oil-bodies absent ..... *R. latifrons* (Lindb.) Lindb.
2. Dioicous; thallus minute (0.2-0.4 mm wide), dark green to brownish; branching palmate, ascending; oil-bodies present ..... *R. palmata* (Hedw.) Carruth.

Key 4: *Pellia* Raddi

1. Thallus without vertical band-like thickenings on section ..... *P. endiviifolia* (Dicks.) Dumort.
1. Thallus with vertical brown colored band-like thickenings on section 2
2. Paroicous; involucre reduced to semi-cylindrical scalelike flap; thallus 8-15 mm wide, 3-7 cm long ..... *P. epiphylla* (L.) Corda
2. Dioicous; involucre forming complete tube; thallus 4-6 mm wide, 1-3 cm long ..... *P. neesiana* (Gottsche) Limpr.

Key B. General key to Leafy (Foliose) Liverworts (Jungermanniales except in *Fossombronia*)

1. Stem-like costa and lamina deeply divided into leaf-like lobes (thallus-like) ..... *Fossombronia foveolata* Lindb.
1. Stem is distinct and leaves arranged in two or three rows 2
2. Leaves composed of filiform segments or leaf margins long ciliate 3
2. Leaves undivided or lobed 4
3. Leaves composed of filiform segments, lobes divided into 3-4 unbranched, unistratose segments ..... Key 17: *Blepharostoma*
3. Leaves 2-6-lobed, leaf margins long ciliated ..... Key 18: *Ptilidium*
4. Leaves complicate (folded)-bilobed 5
4. Leaves not complicate-bilobed 8
5. Ventral lobes larger than dorsal lobes 6
5. Ventral lobes smaller than dorsal lobes 7
6. Ventral lobes narrowly lingulate, parallel-sided ..... *Diplophyllum taxifolium* (Wahlenb.) Dumort.
6. Ventral lobes lingulate or narrowly ovate, rarely parallel-sided ..... Key 12: *Scapania*
7. Underleaves absent; keel region of leaf inflated; perianth dorsiventrally compressed ..... *Radula complanata* (L.) Dumort.
7. Underleaves present; keel region of leaf very short or vestigial; perianth rarely dorsiventrally compressed ..... Key 19: *Porella*
8. Underleaves present 9
8. Underleaves absent (sometimes inconspicuous) 22
9. Leaves and underleaves similar in size and shape ..... Key 15: *Anthelia*
9. Leaves much larger than underleaves 10
10. Leaves incubous 11
10. Leaves succubous, transversely or obliquely inserted 12
11. Leaves entire or rarely bidentate ..... Key 16: *Calypogeia*
11. Leaves 2-6-lobed ..... *Lepidozia reptans* (L.) Dumort.
12. Leaves obliquely inserted ..... Key 4: *Leiocolea*
12. Leaves succubous, transversely inserted 13
13. Leaves undivided (rarely divided in branch leaves of *Chiloscyphus* or notch form) 14
13. Leaves bifid or variously lobed 17
14. Leaf margins with few to many teeth (sometimes absent) ..... *Plagiochila porelloides* (Nees) Lindenb.
14. Leaf margins entire 15
15. Underleaves similar to leaves ..... *Hygrobiella laxifolia* (Hook.) Spruce
15. Underleaves smaller than leaves or absent 16
16. Leaves quadrate-rotundate, underleaves absent or inconspicuous ..... *Jamesoniella autumnalis* (DC.) Steph.
16. Leaves subreniform to orbicular-ovate; underleaves lanceolate to subulate ..... Key 7: *Nardia*
17. Underleaves few, subulate ..... *Gymnocolea inflata* (Huds.) Dumort.
17. Underleaves abundant, ovate-lanceolate 18
18. Underleaves with a tooth on the lobe 19
18. Underleaves without a tooth on the lobe (occasionally with a lateral tooth in *Harpanthus*) 21

19. Underleaves often connate with leaves ..... Key 11: *Lophocolea*
19. Underleaves free 20
20. Underleaves bilobed ..... Key 10: *Chiloscyphus*
20. Underleaves ovate to ovate-lanceolate ..... *Pleurocladula albescens* (Hook.) Grolle
21. Underleaves lanceolate-triangular, apex acute to acuminate ..... *Harpanthus flotovianus* (Nees) Nees
21. Underleaves bilobed (almost to base) into 2 long subulate segments ..... *Geocalyx graveolens* (Schrad.) Nees
22. Outer layer of stem with large, pellucid cells (hyalodermis) which appear clear; leaf cells also pellucid ..... Key 14: *Cephalozia*
22. Outer layer of stem without distinct pellucid cells; appearing opaque; leaf cells not pellucid 23
23. Leaves scarcely broader than stem ..... Key 13: *Cephaloziella*
23. Leaves distinctly broader than stem 24
24. Shoot usually julaceous; leaves spreading horizontally to appressed 25
24. Shoot not julaceous; leaves concave, secund or horizontally spreading 26
25. Leaves distant; leaf margins entire ..... Key 9: *Marsupella*
25. Leaves imbricate; leaf margins crenulate (except *G. concinnatum*) ..... Key 8: *Gymnomitrion*
26. Leaves unlobed ..... Key 6: *Jungermannia*
26. Leaves lobed 27
27. Leaves 2-lobed, broadest at base ..... Key 1: *Anastrophyllum*
27. Leaves 2-4-lobed, broadest at middle 28
28. Leaves unequally divided into 2-3 lobes ..... Key 5: *Tritomaria*
28. Leaves equally divided into 2-4 lobes 29
29. Leaves (2)3-4-lobed, lobes broader, triangular ..... Key 2: *Barbilophozia*
29. Leaves 2(3-4)-lobed, lobes acute-obtuse ..... Key 3: *Lophozia*

Key 1: *Anastrophyllum* (Spruce) Steph.

1. Plants minute (less than 0.1 mm wide); gemmae quadrangular, 1-celled, vinaceous; occurring on decayed wood ..... *A. hellerianum* (Lindenb.) R. M. Schust.
1. Plants medium-sized (1.0-2.0 mm wide); gemmae irregular, 2-4 celled, reddish; occurring on rocks 2
2. Leaves strongly spreading, cells subisodiametric with distinct trigones (often confluent); gemmae 2-celled, light-red to purplish ..... *A. michauxii* (F. Weber) Buch
2. Leaves erect spreading, cells subquadrate without trigones; gemmae 2-4 celled, bright red ..... *A. minutum* (Schreb.) R. M. Schust.

Key 2: *Barbilophozia* Loeske

1. Leaves concave, obliquely inserted 2
1. Leaves nearly flat, horizontally inserted 6
2. Leaves mostly 2 (rarely 3,4)-lobed, sinus descending 1/2-3/5 of their length 3
2. Leaves mostly 3 (rarely 2,4)-lobed, sinus descending 1/4-1/3 of their length 5
3. Leaves usually 4-lobed, lobes narrowly triangular, sinus descending 3/5 of their length ..... *B. quadriloba* (Lindb.) Loeske
3. Leaves usually 2-3-lobed, lobes broadly ovate-triangular, sinus descending less than 1/2 of their length 4
4. Lobes usually 3-lobed, sinus descending less than 1/3 of their length, lobes sharply acute ..... *B. floerkei* (F.Weber & D. Mohr) Loeske
4. Lobes 2-4-lobed, sinus descending ca. 1/2 of their length, lobes blunt to subacute ..... *B. kunzeana* (Huebener) Müll. Frib.

5. Plants with attenuated erect shoots, whose leaves are smaller and appressed; leaves 2-3-lobed, sinus descending 1/4 of their length; collenchyma of leaf cells indistinct (trigones small) ..... *B. attenuata* (Mart.) Loeske
5. Plants without attenuated, erect shoots, whose leaves are smaller and appressed; leaves 3-4-lobed, sinus descending 1/4-1/3 of their length; collenchyma of leaf cells distinct (trigones bulging to confluent) ..... *B. atlantica* (Kaal.) Müll. Frib.
6. Leaves nearly quadrate, without cilia at postical base; apex of lobes round to obtuse ..... *B. barbata* (Schreb.) Loeske
6. Leaves narrowed toward base with cilia at postical base; apex of lobes acute to mucronate 7
7. Plants small (1.0-2.5 mm wide, 2-5 cm long); apex of lobes acute to apiculate, cilia at postical base few (2-5), short; gemmae abundant ..... *B. hatcheri* (A.Evans) Loeske
7. Plants large (3.0-5.0 mm wide, 5-8 cm long); apex of lobes mucronate, cilia at postical base numerous (5-8), long; gemmae absent (rarely developed) ..... *B. lycopodioides* (Wallr.) Loeske

Key 3: *Lophozia* (Dumort.) Dumort

1. Medulla of stem dorsiventrally differentiated, with mycorrhizae; oil bodies fewer (ca. 5-20 per cell) 2
1. Medulla of stem homogenous, free of mycorrhizae; oil bodies numerous (ca. 20-50 per cell) 8
2. Paroicous ..... *L. excisa* (Dicks.) Dumort.
2. Dioicous 3
3. Trigones strongly bulging; gemmae mostly absent ..... *L. longiflora* (Nees) Schiffn.
3. Trigones minute; gemmae abundant 4
4. Perianth longly exserted; androecia terminal (intercalary) 5
4. Perianth cylindrical-ovate; androecia intercalary 6
5. Oil-bodies 4-10 per cell; gemmae reddish brown ..... *L. longidens* (Lindb.) Macoun
5. Oil-bodies 10-16(20) per cell; gemmae greenish ..... *L. ventricosa* (Dicks.) Dumort.
6. Plants ascending; leaf sinus 1/3-1/2 ..... *L. ascendens* (Warnst.) R.M.Schust.
6. Plants prostrate; leaf sinus 1/4-1/10 7
7. Leaves strongly concave; gemmae pale green ..... *L. wenzelii* (Nees) Steph.
7. Leaves flat; gemmae reddish ..... *L. sudetica* (Nees ex Huebener) Grolle
8. Leaf-lobes rounded or obtuse; underleaves present ..... *L. obtusa* (Lindb.) A.Evans
8. Leaf-lobes acute; underleaves absent 9
9. Perianth mouth lobulate with setaceous cilia ..... *L. incisa* (Schrad.) Dumort.
9. Perianth mouth subentire or denticulate without setaceous cilia ..... *L. opacifolia* Culm. ex Meyl.

Key 4: *Leiocolea* (Müll. Frib.) H. Buch

1. Paroicous 2
1. Dioicous 3
2. Lobes never pluriciliate; beak of perianth long; underleaves subulate to lanceolate ..... *L. gillmanii* (Austin) R. M. Schust.
2. Lobes pluriciliate; beak of perianth short; underleaves very large, 2-3-fid ..... *L. rutheana* (Limpr.) M. Howe
3. Plants small (less than 1 mm wide and 12 mm long); underleaves absent ..... *L. badensis* (Gottsche) Schiffn.
3. Plants large (over 1-5 mm wide and 1-8 cm long); underleaves present 4

4. Gemmae present ..... *L. heterocolpos* (Thed. ex Hartm.) M. Howe
4. Gemmae absent 5
5. Leaves 0.15-0.25 bilobed; cells large, ca. 35-40 x 40-55 µm in midleaf ..... *L. bantriensis* (Hook.) Steph.
5. Leaves 0.25-0.35 bilobed; cells small, ca. 25-30 x 25-35 µm in midleaf ..... *L. collaris* (Nees) Dumort.

Key 5: *Tritomaria* Loeske

1. Leaves symmetric, equally trilobed with blunt to rounded apices; perianth mouth entire or subentire ..... *T. polita* (Nees) Jørg.
1. Leaves asymmetric, unequally 2-3-lobed with acute or acuminate apices; perianth mouth strongly dentate 2
2. Leaves plane, wider than long; gemmae rare, yellowish to yellowish-brown ..... *T. quinquedentata* (Huds.) H. Buch
2. Leaves canaliculate-complanate, longer than wide; gemmae abundant, reddish-brown to rust-red 3
3. Leaves usually subequally trilobed, lobes acute to subacute; trigones large; cilia of perianth mouth 2-4 cells long; gemmae reddish-brown, sharply polygonal ..... *T. scitula* (Taylor) Jørg.
3. Leaves asymmetrically 2-3 lobed, lobes acute or acuminate; trigones small; cilia of perianth mouth 5-6 cells long; gemmae rust-red, elliptical to irregularly polygonal 4
4. Gemmae smooth, ovoid-ellipsoidal; leaf cells 10-15 x 15-25 µm in midleaf; cell walls thick, trigones not bulging ..... *T. exsecta* (Schmidel) Loeske
4. Gemmae angulate, polygonal; leaf cells 15-20 x 20-40 µm in midleaf; cell walls thin, trigones bulging ..... *T. exsectiformis* (Breidl.) Loeske

Key 6: *Jungermannia* L.

1. Perianth abruptly narrowed distally into a beaked mouth 2
1. Perianth gradually narrowed, unbeaked 4
2. Perianth tubular, smooth; leaves ovate oblong, parallel-sided ..... *J. leiantha* Grolle
2. Perianth cylindrical, ovoid to clavate; leaves reniform-orbicular to slightly ovate, erecto-patent 3
3. Paroicous; plants pure greenish; leaves orbicular to orbicular-cordate; leaf cells 25-30 x 35-50 µm in midleaf ..... *J. sphaerocarpa* Hook.
3. Dioicous; plants at least partly reddish purple; leaves rounded or ovate; leaf cells 20-25 x 25-35 µm in midleaf ..... *J. rubra* Underw.
4. Perianth plicate for nearly almost the entire length, with isodiametric cells, perigynium lacking; rhizoids usually colorless 5
4. Perianth plicate above only, with elongated cells; perigynium present; rhizoids sometimes reddish-purple 8
5. Paroicous 6
5. Dioicous 7
6. Perianth obovoid; leaves ovate-cordate, cells 15-20 x 15-25 µm in midleaf ..... *J. polaris* Lindb.
6. Perianth fusiform; leaves broadly elliptical, cells 20-25 x 25-30 µm in midleaf ..... *J. pumila* With.
7. Plants 0.8-1.0 mm wide, 0.2-3.0 cm long; perianth ovoid or oblong-ovoid ..... *J. atrovirens* Dumort.
7. Plants 2.0-4.0 mm wide, 2-12 cm long; perianth slender fusiform ..... *J. exsertifolia* Steph. subsp. *cordifolia* (Dumort.) Váña

8. Paroicous; plants 2.0-2.5 mm wide, 2.0-5.0 cm long; leaves broadly ovate; rhizoids purple; plants strongly fragrant ..... *J. obovata* Nees
8. Dioicous; plants 1.5-2.0 mm wide, 0.5-2.0 cm long; leaves suborbicular to broadly reniform-orbicular, rhizoids reddish; nonaromatic ..... *J. hyalina* Lyell

Key 7: *Nardia* Gray

1. Leaves distinctly bilobed ..... *N. breidleri* (Limpr.) Lindb.
1. Leaves entire-emarginate 2
2. Plants robust, 2.0-3.0 mm wide, 2.0-15 cm long; branching ventral; leaves entire, erect-appressed ..... *N. compressa* (Hook.) Gray
2. Plants small to large, 1.0-2.5 mm wide, 0.5-5.0 cm long; branching lateral-terminal; leaves entire to emarginate; never erect-appressed 3
3. Dioicous; plants large, 1.0-2.5 mm wide, 1.0-5.0 cm long, pale green; cells large, 25-30 x 30-40 µm in midleaf; oil-bodies glistening and homogenous ..... *N. scalaris*
3. Paroicous; plants small, 0.8-1.5 mm wide, 5-10 mm long, brownish; cells small, 20-25 x 25-30 µm in midleaf; oil-bodies granular and opaque ..... *N. geoscyphus* (De Not.) Lindb.

Key 8: *Gymnomitrion* Corda

1. Plants 5-6 mm long; leaf-lobes acute, margins entire, bilobed for 0.20-0.35 their length, sinus acute and open; trigones bulging into cells ..... *G. concinnatum* (Lightf.) Corda
1. Plants 1-2 cm long; leaf-lobes roundish, margins crenulate, bilobed for 0.15-0.25 their length, sinus obtuse and closed; trigones not bulging into cells ..... *G. obtusum* Lindb.

Key 9: *Marsupella* Dumort.

1. Plants green or with red pigments; leaves with reflexed margins, 0.1-0.3 bilobed, leaf- sinus broad, obtuse to acute ..... *M. emarginata* (Ehrh.) Dumort.
1. Plants deep dull green, brownish above; leaf margins never reflexed, 0.3-0.6 bilobed leaf-sinus acute ..... *M. sphacelata* (Lindenb.) Dumort.

Key 10: *Chiloscyphus* Corda

1. Plant body transparent, pale whitish to yellowish-green; cells 35-40 x 45-60 µm in midleaf; perianth lobes spinose dentate ..... *C. pallescens* (Hoffm.) Dumort.
1. Plant body dull to deep-green; cells 25-30 x 30-35 µm at midleaf; perianth lobes entire or undulate ..... *C. polyanthos* (L.) Corda

Key 11: *Lophocolea* (Dumort.) Dumort.

1. Leaves ovate-triangular, leaf-lobes terminated by a row of superposed cells; gemmae lacking ..... *L. bidentata* (L.) Dumort.
1. Leaves short-oblong, leaf-lobes never terminating in a row of superposed cells; gemmae present 2
2. Plants pale whitish-green; leaves entire-subentire to bilobed (shallowly); gemmae rarely developed ..... *L. heterophylla* (Schrad.) Dumort.
2. Plants greenish-yellow; leaves bilobed 0.20-0.35 of their length; gemmae always abundantly developed at leaf margins ..... *L. minor* Nees

Key 12: *Scapania* (Dumort.) Dumort.

1. Base of dorsal lobes with coarse teeth 2

1. Base of dorsal lobe entire or with minute teeth 3
2. Teeth of dorsal, basal leaf margins strongly developed with antleroid branching; on earth and on decayed wood ..... *S. bolanderi* Austin
2. Teeth of leaf margins unbranched; on earth and rarely on decayed wood ..... *S. americana* Müll. Frib.
3. Ventral lobes non-decurrent 4
3. Ventral lobes conspicuously decurrent 6
4. Ventral lobes falcate; gemmae abundant on all leaves; oil-bodies solitary, persistent ..... *S. gymnostomophila* Kaal.
4. Ventral lobes oblong-ovate to broadly cordate; gemmae on tips of shoot; oil-bodies over 2, dissipating 5
5. Ventral lobes broadly cordate; gemmae reddish or reddish brown ..... *S. paludicola* Loeske & Müll. Frib.
5. Ventral lobes oblong-obcordate; gemmae greenish ..... *S. irrigua* (Nees) Nees
6. Margins of leaves with equally thickened, 2-4-cells rows as a differentiated border ..... *S. curta* (Mart.) Dumort.
6. Margins of leaves with thin-walled cells, not forming a differentiated border 7
7. Dorsal lobes weakly concave-arched or arcuately inserted 8
7. Dorsal lobes transversely inserted 10
8. Dorsal lobes more sharply acute than ventral lobes ..... *S. mucronata* H. Buch
8. Dorsal lobes similar in shape to ventral lobes 9
9. Dorsal lobes weakly concave-arched; restricted to decayed wood ..... *S. apiculata* Spruce
9. Dorsal lobes strongly arched; restricted to seepage-moistened rocks ..... *S. uliginosa* (Müll. Frib.) Müll. Frib.
10. Dorsal lobes ca. 7.0 to 8.0 the ventral in size 11
10. Dorsal lobes ca. 0.35 to 0.65 the ventral in size 12
11. Plants small (ca. 2 mm wide, 8-12 mm long); leaf margins entire ..... *S. cuspiduligera* (Nees) Müll. Frib.
11. Plants large (ca. 2-4 mm wide, up to 5 cm long); leaf margins finely denticulate ..... *S. subalpina* (Nees) Dumort.
12. Plants large (up to 5 mm wide, 20 cm long); leaf-lobes variable ..... *S. undulata* (L.) Dumort.
12. Plants small (ca. 1.0-1.5 mm wide, 3-10 mm long); leaf-lobes stable 13
13. Apex of ventral lobes round to obtuse; leaf cells isodiametric, with bulging trigones ..... *S. saxicola* R. M. Schust.
13. Apex of ventral lobes acute; leaf cells rectangular, with concave trigones ..... *S. glaucocephala* (Taylor) Austin

Key 13: *Cephaloziella* (Spruce) Schiffn.

1. Leaves deeply bilobed, up to 0.8 length; lobes 2-4 cells wide at base ; underleaves always present on sterile shoots ..... *C. subdentata* Warnst.
1. Leaves moderately bilobed, less than 0.6 length; lobes 4-10 cells wide at base; underleaves absent or present 2
2. Leaves often dentate; underleaves present and distinct on sterile shoots ..... *C. divaricata* (Sm.) Schiffn.
2. Leaves edentate; underleaves absent or minute if present 3
3. Leaf-lobes oval-lanceolate, 3-8 cells wide at base, cells strongly thick-walled; gemmae 1-2 celled, ovoid, green ..... *C. rubella* (Nees) Warnst.
3. Leaf-lobes ovate-triangular, 5-8 cells wide at base, cells thin walled; gemmae 2-celled, ellipsoidal, pale green ..... *C. hampeana* (Nees) Schiffn.

Key 14: *Cephalozia* (Dumort.) Dumort.

1. Leaves distinctly decurrent, orbicular (as wide as long), horizontally or obliquely inserted, bilobed (0.2-0.5 of their length), lobes connivent 2
1. Leaves never distinctly decurrent, ovate (longer than wide), subtransversely inserted, bilobed (0.5-0.7 of their length), lobes never connivent 4
2. Dioicous; leaf cells 15-35 x 20-35 µm at base; stolons absent .... *C. lunulifolia* (Dumort.) Dumort.
2. Autoicous; leaf cells 30-50 x 45-60 µm at base; stolons frequent or absent 3
3. Leaves strongly decurrent, 8-12 cells wide, with sharply pointed connivent lobes, cells 40-50 x 45-60 µm; stolons absent; perianth mouth with acuminate lobes which terminate in 2-4 elongate cells ... *C. connivens* (Dicks.) Lindb.
3. Leaves slightly decurrent, 12-25 cells wide, with short pointed little connivent lobes, cells 30-35 x 40-50 µm; stolons frequent; perianth mouth shortly crenulate ..... *C. pleniceps* (Austin) Lindb.
4. Dioicous; cortical cells of stem in 7-10 rows; leaves transverse, 4-10 cells wide at base 5
4. Autoicous; cortical cells of stem in 6-12 rows; leaves subtransverse-subhorizontal, 4-6 cells wide at base 7
5. Cortical stem cells 7 rows; leaves 4 cells wide at base; leaf-lobes strongly attenuated ..... *C. lacinulata* Spruce
5. Cortical cells 10 rows; leaves 5-10 cells wide at base; leaf-lobes subparallel 6
6. Leaf-lobes narrow and long, 3-4 cells wide at base, bilobed for ca. 0.7 of their length ..... *C. macounii* (Austin) Lindb.
6. Leaf-lobes lanceolate-triangular, 4-5 cells wide at base, bilobed for ca. 0.5 of their length ..... *C. leucantha* Spruce
7. Cortical cells 6-7 rows; leaf-lobe 3-4 cells wide at base; always fertile ..... *C. loitlesbergeri* Schiffn.
7. Cortical cells 8-12 rows; leaf-lobe 5-10 cells wide at base 8
8. Leaf cells 30-40 x 40-50 µm at leaf base, with thin pigmented walls; perianth mouth denticulate ..... *C. bicuspidata* (L.) Dumort.
8. Leaf cells 20-25 x 20-35 µm at leaf base, with thick brownish-golden walls; perianth mouth crenulate ..... *C. ambigua* C. Massal.

Key 15: *Anthelia* (Dumort.) Dumort.

1. Dioicous; plants dark green, dark yellowish-green, 7.0-40 mm long (slender); cell walls thick; perianth oblong ..... *A. julacea* (L.) Dumort.
1. Paroicous; plants silvery gray, grayish-green, 2.0-10 mm long (compact); cell walls thin; perianth ovate ..... *A. juratzkana* (Limpr.) Trevis

Key 16: *Calypogeia* Raddi

1. Oil-bodies distinctly deep blue ..... *C. azurea* Stotler & Crotz
1. Oil-bodies hyaline to slightly grayish or colorless 2
2. Underleaves undivided, or shallowly (less than 1/4 of length) divided into two lobes ..... *C. integristipula* Steph.
2. Underleaves deeply (over 1/2 of length) divided into two lobes 3
3. Leaf cells large (over 30 µm in apices, 35-50 x 45-75 µm in midleaf); underleaves 1-2 times wider than stem ..... *C. muelleriana* (Schiffn.) Müll. Frib.
3. Leaf cells small (less than 30 µm in apices, 25-35 x 30-45 µm in midleaf); underleaves 2-3.5 times wider than stem 4
4. Leaf cells 20-35 x 25-40 µm in midleaf, thin-walled; underleaves slightly longer than wide, ca. 1.2-2 times wider than stem,

bilobed to 0.6-0.8 length; on *Sphagnum* ..... *C. sphagnicola* (Arnell & J. Perss.) Warnst. & Loeske
4. Leaf cells 25-30 x 30-45 µm in midleaf, isodiametric, collenchymatous; underleaves ca. 2-3.5 times wider than stem, bilobed to 0.4-0.6 length; on decaying wood ..... *C. suecica* (Arnell & J. Perss.) Müll. Frib.

Key 17: *Blepharostoma* (Dumort.) Dumort.

1. Plants distantly branched; leaves 2-3-lobed, leaf cells ca. 25-50 µm wide, 45-110 µm long ..... *B. arachnoideum* M. Howe
1. Plants sparingly branched; leaves 3-4 lobed, leaf cells ca. 15-25 µm wide, 40-70 µm long 2
2. Leaf cells elongate, usually 15-20 µm wide, 30-60 µm long; nonarctic ..... *B. trichophyllum* subsp. *trichophyllum*
2. Leaf cells nearly quadrate, usually 20-25 µm wide, 20-30 µm long; arctic ..... *B. trichophyllum* subsp. *brevirete* (Bryhn & Kaal.) R. M. Schust.

Key 18: *Ptilidium* Nees

1. Leaf-lobes usually 1-2-ciliate at margin; underleaves deeply lobed (up to 7/8 of their length) ..... *P. californicum* (Austin) Underw.
1. Leaf-lobes usually multiciliate at margin; underleaves rather moderately lobed (up to 1/3 to 1/2 of their length) 2
2. Stems prostrate; leaves densely crowded, dorsal lobe 6-10 cells wide at base; on trees and decayed wood ..... *P. pulcherrimum* (Weber) Vain
2. Stems erect; leaves loosely crowded, dorsal lobe 15-20 cells wide at base; on sandy soil and rocks ..... *P. ciliare* (L.) Hampe

Key 19: *Porella* L.

1. Ventral lobes long-decurrent, margins strongly reflexed; underleaves 2 times as wide as ventral lobes ..... *P. cordaeana* (Huebener) Moore
1. Ventral lobes non- or only short-decurrent, margins plane or weakly reflexed; underleaves 1-2 times as wide as ventral lobes 2
2. Underleaves about 2 times as wide as ventral lobes; gametophores glossy; margins of ventral lobes entire; trigones moderate ..... *P. roellii* Steph.
2. Underleaves about as wide as ventral lobes; gametophores glossy to dull; margins of ventral lobes recurved; trigones small to large (bulging) 3
3. Trigones strongly bulging into cell lumina; margins of ventral lobes reflexed; apex of underleaves usually rounded ..... *P. navicularis* (Lehm. & Lindenb.) Pfeiff.
3. Trigones not bulging into cell lumina; margins of ventral lobes plane; apex of underleaves usually reflexed 4
4. Underleaves distinctly wider than ventral lobes; postical leaf-base flat; ventral lobes narrowly ovate-triangular to lanceolate, apex tapered; perianth mouth with unbranched cilia; elaters 2-spiraled ..... *P. platyphylla* (L.) Pfeiff.
4. Underleaves about as wide as ventral lobes; postical leaf-base strongly crispate; ventral lobes oblong-lingulate to ovate, apex narrowly reflexed; perianth mouth with crowded branched cilia; elaters 1-spiraled ..... *P. platyphylloides* (Schwein.) Lindb.
(Váña referred conspecific with *P. platyphylla*)

Excluded Species

Chiloscyphus pallescens (Ehrh. ex Hoffm.) Dumort. var. *fragilis* (Roth) Müll. Frib.
Chiloscyphus polyanthos (L.) Corda var. *rivularis* (Schrad.) Nees

The above two varieties have been reported for Montana based on color of plant body, size of leaf cells, and shape of leaves. These characters are easily influenced by habitat and unreliable to separate the taxa of *Chiloscyphus* as indicated by Schuster (1980), Smith (1990), and Hong (1993).

Jungermannia (*Solenostoma*) *gracillima* Sm.

The species was listed for Montana, however, all specimens cited as *J. gracillima* are actually *J. rubra* (Váña and Hong 1999).

Scapania nemorea (L.) Grolle [= *S. nemorosa* (L.) Dumort.]

The species has been reported for Montana; however, *S. nemorea* is confined to the eastern half of the continent and does not occur in western North America (Schuster 1974, Hong 1980).

Distribution

Table 1 indicates occurrence of each taxon in some plant association in Montana and a literature reference.

TABLE 1. Occurrence of each taxon in some plant association in Montana.

Taxon	Occurrence (forest and area)	Source
Anastrophyllum hellerianum	fir-hemlock-pine (west, central)	Hong 1975
Anastrophyllum michauxii	hemlock-redcedar (west)	Hong 1975
Anastrophyllum minutum	fir-hemlock-spruce (west)	Hong 1975
Aneura pinguis	fir-hemlock-spruce (west)	Hong 1977
Anthelia julacea	alpine (Glacier Co.)	Jones 1910
Anthelia juratzkana	alpine (Glacier Co.)	Hermann 1969
Apometzgeria pubescens	hemlock-spruce-redcedar (west)	Jones 1910
Asterella gracilis	hemlock-spruce-redcedar (west)	Jones 1910
Asterella lindenbergiana	hemlock-spruce (west)	Clark and Frye 1928
Asterella saccata	hemlock-spruce-redcedar (west)	Clark and Frye 1928
Athalamia hyalina	hemlock-spruce (west)	Clark and Frye 1937-1947
Barbilophozia atlantica	fir-hemlock (west)	Hong 1975
Barbilophozia attenuata	hemlock-redcedar (west)	Clark and Frye 1928
Barbilophozia barbata	fir-hemlock-spruce (west)	Hong 1975
Barbilophozia floerkei	alpine (Glacier Co.)	Jones 1910
Barbilophozia hatcheri	fir-hemlock-pine (widespread)	Hong 1975
Barbilophozia kunzeana	fir-hemlock-spruce (west)	Hong 1975
Barbilophozia lycopodioides	alpine (Glacier Co.)	Jones 1910
Barbilophozia quadriloba	fir-hemlock-spruce (west)	Hong 1975
Blasia pusilla	riparian (west)	Hong 1977
Blepharostoma arachnoideum	alpine (Glacier Co.)	Clark and Frye 1928
Blepharostoma trichophyllum subsp. *trichophyllum*	fir-hemlock-pine (west, central)	Hong 1975
Blepharostoma trichophyllum subsp. *brevirete*	alpine (Glacier Co.)	Hermann 1969
Calypogeia azurea	fir-hemlock-redcedar (west)	Hong 1975
Calypogeia integristipula	fir-hemlock-spruce (west)	Hong 1975
Calypogeia muelleriana	fir-hemlock-spruce (west, central)	Hong 1975
Calypogeia sphagnicola	bog (extreme west)	Hong 1975
Calypogeia suecia	fir-hemlock-pine (west, central)	Hong 1975
Cephalozia ambigua	alpine (west)	Hong 1975
Cephalozia bicuspidata	fir-hemlock-pine (west, central)	Hong 1975

Continued, next page

TABLE 1, cont'd

Taxon	Occurrence (forest and area)	Source
Cephalozia connivens	fir-hemlock-spruce (west, central)	Hong 1975
Cephalozia lacinulata	fir-hemlock-spruce (west)	Hong 1975
Cephalozia leucantha	hemlock-redcedar-spruce (west)	Hermann 1969
Cephalozia loitlesbergeri	fir-hemlock-spruce (west)	Hong 1975
Cephalozia lunulifolia	fir-hemlock-pine (widespread)	Hong 1975
Cephalozia macounii	fir-hemlock-spruce-red cedar (west)	Hong 1975
Cephalozia pleniceps	fir-hemlock-spruce-pine (west)	Hong 1975
Cephaloziella divaricata	fir-hemlock-spruce (west)	Hong 1975
Cephaloziella hampeana	fir-hemlock-spruce (west)	Hong 1975
Cephaloziella rubella	fir-hemlock-spruce (west)	Hong 1975
Cephaloziella subdentata	alpine (Glacier Co.)	Hermann 1969
Chiloscyphus pallescens	fir-hemlock-spruce (west, central)	Hong 1975
Chiloscyphus polyanthos	fir-hemlock-pine (widespread)	Hong 1975
Conocephalum conicum	fir-hemlock-pine (widespread)	Hong 1977
Diplophyllum taxifolium	fir-hemlock-pine (west, central)	Hong 1975
Fossombronia foveolata	alpine (Glacier Co.)	Hermann 1969
Gymnocolea inflata	alpine (Glacier Co.)	Hermann 1969
Geocalyx graveolens	fir-hemlock-pine (west, central)	Hong 1975
Gymnomitrion concinnatum	alpine (Flathead Co.)	Hermann 1969
Gymnomitrion obtusum	alpine (Glacier Co.)	Jones 1910
Harpanthus flotovianus	alpine (Glacier Co.)	Jones 1910
Hygrobiella laxifolia	alpine (Glacier Co.)	Hermann 1969
Jamesosniella autumnalis	fir-hemlock-spruce (west, central)	Hong 1975
Jungermannia atrovirens	hemlock-redcedar-spruce (west)	Hong 1975
Jungermannia exsertifolia subsp. *cordifolia*	fir-hemlock-spruce (west, central)	Hong 1975
Jungermannia leiantha	fir-hemlock-pine (west, central)	Hong 1975
Jungermannia obovata	alpine (Glacier Co.)	Clark and Frye 1928
Jungermannia hyalina	fir-hemlock-spruce (west)	Hong 1975
Jungermannia polaris	fir-hemlock-spruce (west)	Hong 1975
Jungermannia sphaerocarpa	fir-hemlock-spruce (west, central)	Hong 1975
Jungermannia pumila	fir-hemlock-pine (west, central)	Hong 1975
Jungermannia rubra	fir-hemlock-spruce (west)	Hong 1975
Leiocolea badensis	alpine (Glacier Co.)	Clark and Frye 1928
Leiocolea bantriensis	fir-hemlock-redcedar (west, central)	Hong 1975
Leiocolea collaris	fir-hemlock-pine (west, central)	Hong 1975
Leiocolea gillmanii	fir-hemlock-spruce (west, central)	Hong 1975
Leiocolea heterocolpos	fir-hemlock-spruce (west, central)	Hong 1975
Leiocolea rutheana	hemlock-redcedar (west)	Hong 1975
Lepidozia reptans	fir-hemlock-pine-spruce (widespread)	Hong 1975
Lophocolea bidentata	fir-hemlock-pine-spruce (west)	Hong 1975
Lophocolea heterophylla	fir-hemlock-pine-spruce (west)	Hong 1975
Lophocolea minor	fir-hemlock-pine (west, central)	Hong 1975
Lophozia ascendens	fir-hemlock-pine (west, central)	Hong 1975
Lophozia excisa	fir-hemlock-spruce (west)	Hong 1975
Lophozia incisa	fir-hemlock-pine (widespread)	Hong 1975
Lophozia longidens	fir-hemlock-pine (west, central)	Hong 1975
Lophozia longiflora	fir-hemlock-pine (west, central)	Hong 1975
Lophozia obtusa	fir-hemlock-pine (west, central)	Hong 1975
Lophozia opacifolia	alpine (west)	Hong 2002
Lophozia sudetica	alpine (extreme west)	Clark and Frye 1928
Lophozia ventricosa	fir-hemlock-pine (widespread)	Hong 1975
Lophozia wenzelii	alpine (Glacier Co.)	Hermann 1969

Taxon	Occurrence (forest and area)	Source
Lunularia cruciata	greenhouse (west)	Hong 1977
Mannia fragrans	spruce-redcedar (west)	Hermann 1969
Marchantia polymorpha	fir-hemlock-pine (widespread)	Hong 1977
Marsupella emarginata	fir-hemlock-spruce-redcedar (west)	Hong 1975
Marsupella sphacelata	alpine (Glacier Co.)	Jones 1910
Metzgeria conjugata	hemlock-spruce-pine (west, central)	Hong 1977
Nardia breidleri	alpine (Glacier Co.)	Clark and Frye 1938
Nardia compressa	hemlock-spruce-redcedar (west)	Hong 1975
Nardia geoscyphus	alpine (Glacier Co.)	Frye and Clark 1928
Nardia scalaris	fir-hemlock-spruce (west)	Hong 1975
Pellia endiviifolia	fir-hemlock-pine (west, central)	Hong 1977
Pellia epiphylla	fir-hemlock-spruce (west)	Clark and Frye 1937
Pellia neesiana	fir-hemlock-spruce-redcedar (west)	Clark and Frye 1928
Plagiochila porelloides	fir-hemlock-spruce-pine (widespread)	Hong 1975
Pleurocladula albescens	alpine (Glacier Co.)	Hermann 1969
Porella cordaeana	fir-hemlock-spruce-pine (west, central)	Hong 1975
Porella navicularis	fir-hemlock-spruce (west)	Hong 1975
Porella platyphylla	fir-hemlock-redcedar (west)	Hong 1975
Porella platyphylloidea	fir-hemlock-spruce-pine (west)	Hong 1975
Porella roellii	fir-hemlock-spruce-pine (west)	Hong 1975
Preissia quadrata	fir-hemlock-pine (west, central)	Hong 1977
Ptilidium californicum	fir-hemlock-spruce-redcedar (west)	Hong 1975
Ptilidium ciliare	alpine (Glacier Co.)	Frye and Clark 1937-1947
Ptilidium pulcherrimum	fir-hemlock-pine-spruce (widespread)	Hong 1975
Radula complanata	fir-hemlock-redcedar (west, central)	Hong 1975
Reboulia hemisphaerica	fir-hemlock-spruce (west)	Hong 1977
Riccardia latifrons	fir-hemlock-spruce (west)	Hong 1977
Riccardia multifida	fir-hemlock-spruce (west)	Hong 1977
Riccardia palmata	fir-hemlock-spruce (west)	Hong 1977
Riccia cavernosa	hemlock-spruce (extreme west)	Frye and Clark 1937-1947
Riccia fluitans	aquatic (central)	Hong 1977
Riccia frostii	aquatic (central)	Clark and Frye 1928
Riccia sorocarpa	spruce-redcedar (west)	Clark and Frye 1937
Ricciocarpos natans	aquatic (west)	Hong 1977
Scapania americana	fir-spruce (extreme west)	Hong 1975
Scapania apiculata	fir-hemlock-pine (west)	Hong 1975
Scapania bolanderi	fir-hemlock (extreme west)	Hong 1975
Scapania curta	fir-hemlock-spruce (west, central)	Hong 1975
Scapania cuspiduligera	fir-hemlock-pine (west, central)	Hong 1975
Scapania glaucocephala	fir-hemlock-spruce (west, central)	Hong 1975
Scapania gymnostomophila	fir-hemlock-spruce (west)	Hong 1975
Scapania irrigua	fir-hemlock-spruce (west, central)	Hong 1975
Scapania mucronata	fir-hemlock-spruce (west, central)	Hong 1975
Scapania paludicola	fir-hemlock-spruce (west)	Hong 1975
Scapania paludosa	spruce-redcedar (west)	Hong 1975
Scapania saxicola	alpine (Glacier Co.)	Hermann 1969
Scapania subalpina	fir-hemlock-pine (west, central)	Hong 1975
Scapania undulata	fir-hemlock-pine (west, central)	Hong 1975
Tritomaria exsecta	fir-hemlock-pine (west, central)	Hong 1975
Tritomaria exsectiformis	fir-hemlock-pine (west, central)	Hong 1975
Tritomaria polita	fir-hemlock-spruce (west)	Hong 1975
Tritomaria quinquedentata	fir-hemlock-spruce (extreme west)	Hong 1975
Tritomaria scitula	fir-hemlock-spruce (west, central)	Hong 1975

Synonyms

Included are names of species recorded previously for Montana that are now considered synonyms.

Asterella ludwigii auct. = *Asterella gracilis* (Weber) Underw.

Barbilophozia gracilis (Steph.) Müll. Frib. = *Barbilophozia attenuata* (Mart.) Loeske

Calypogeia meylanii H. Buch = *Calypogeia integristipula* Steph.

C. trichomanis auct. non (L.) Corda = *Calypogeia azurea* Stotler & Crotz

Cephalozia affinis Steph. = *Cephalozia lunulifolia* (Dumort.) Dumort.

C. lammersiana (Huebener) Carring. = *Cephalozia bicuspidata* (L.) Dumort.

C. media Lindb. = *Cephalozia lunulifolia* (Dumort.) Dumort.

Cephaloziella byssacea (Roth) Warnst. = *Cephaloziella divaricata* (Sm.) Schiffn.

C. spinigera (Lindb.) Jørg. = *Cephaloziella subdentata* Warnst.

Clevea hyalina (Sommerf.) Lindb. = *Athalamia hyalina* (Sommerf.) S. Hatt.

Fossombronia dumortieri Huebener et Genth ex Lindb. = *Fossombronia foveolata* Lindb.

Grimaldia fragrans (Balbis) Corda = *Mannia fragrans* (Balbis) Frye & L. Clark

Jungermannia lanceolata auct. = *Jungermannia leiantha* Grolle

Leiocolea obtusa (Lindb.) H. Buch = *Lophozia obtusa* (Lindb.) A. Evans

Lophocolea cuspidata (Nees) Limpr. = *Lophocolea bidentata* (L.) Dumort.

Lophozia alpestris auct., (Schleich. ex F. Weber) A. Evans = *Lophozia sudetica* (Nees ex Huebener) Grolle

L. atlantica (Kaal.) Müll. Frib. = *Barbilophozia atlantica* (Kaal.) Müll. Frib.

L. attenuata (Mart.) Dumort. = *Barbilophozia attenuata* (Mart.) Loeske

L. badensis (Gottsche) Schiffn. = *Leiocolea badensis* (Gottsche) Jørg.

L. bantriensis (Hook.) Steph. = *Leiocolea bantriensis* (Hook.) Jørg.

L. collaris (Nees) Dumort. = *Leiocolea collaris* (Nees) Schljakov

L. gillmanii (Austin) R. M. Schust. = *Leiocolea gillmanii* (Austin) A. Evans

L. guttulata (Lindb. et Arnell) A. Evans = *Lophozia longiflora* (Nees) Schiffn.

L. hatcheri (Evans) Steph. = *Barbilophozia hatcheri* (A. Evans) Loeske

L. kiaeri Jørg. = *Lophozia excisa* (Dicks.) Dumort.

L. lycopodioides (Wallr.) Cogn. = *Barbilophozia lycopodioides* (Wallr.) Loeske

L. muelleri (Lindenb.) Dumort. = *Leiocolea collaris* (Nees) Schljakov

L. porphyroleuca (Nees) Schiffn. = *Lophozia longiflora* (Nees) Schiffn.

L. quadriloba (Lindb.) A. Evans = *Barbilophozia quadriloba* (Lindb.) Loeske

Marsupella usutulata (Huebener) Pearson = *Marsupella emarginata* (Ehrh.) Dumort.

Metzgeria pubescens (Schrank) Raddi = *Apometzgeria pubescens* (Schrank.) Kuwah.

Pellia fabbroniana Raddi = *Pellia endiviifolia* (Dicks.) Dumort.

Plagiochila asplenioides (L.) Dumort. subsp. *porelloides* (Nees) R. M. Schust. = *Plagiochila porelloides* (Nees) Lindenb.

Plectocolea obovata (Nees) Mitt. = *Jungermannia obovata* Nees

Pleuroclada albescens (Hook.) Spruce = *Pleurocladula albescens* (Hook.) Grolle

Riccia crystallina auct. non L. = *Riccia cavernosa* Hoffm.

Scapania paludosa (Müll. Frib.) Müll. Frib. = *Scapania uliginosa* (Lindenb.) Dumort. (Zehr 1980)

Solenostoma cordifolium (Dumort.) Steph. = *Jungermannia exsertifolia* Steph. subsp. *cordifolia* (Dumort.) Váňa

S. hyalinum (Lyell) Mitt. = *Jungermannia hyalina* Lyell

S. oblongifolium (Müll. Frib.) Müll. Frib. = *Jungermannia pumila* With.

S. obovatum (Nees) C. Massal. = *Jungermannia obovata* Nees

S. pumilum (With.) Müll. Frib. = *Jungermannia pumila* With.

S. sphaerocarpum (Hook.) Steph. = *Jungermannia sphaerocarpa* Hook.

S. triste (Nees) Müll. Frib. = *Jungermannia atrovirens* Dumort.

Sphenolobus hellerianus (Lindenb.) Steph. = *Anastrophyllum hellerianum* (Lindenb.) R.M. Schust.

S. minutus (Schreb.) Berggr. = *Anastrophyllum minutum* (Schreb.) R. M. Schust.

Acknowledgements

I thank Drs. M. Easton, F. Gilliard, D. Olson, W. Furdell, A. Alt, Rev. J. Sikora, and Sister M. Benoit for their assistance. I am also grateful to Drs. P. Davidson, R. Grolle, J. Váňa, and D. Wagner for suggestions and helpful comments on the original manuscript.

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Received 22 October 2001
Accepted for publication 20 May 2002

Won Shic Hong, Department of Biology, University of Great Falls, Great Falls, Montana 59405-4934 E-mail: whong@ugf.edu

Comparison of Hepatic Flora and Floristic Affinities among Four Neighboring Islands, Queen Charlotte Islands, British Columbia

Abstract

The hepatic flora of Burnaby, Hotspring, Huxley, and Ramsay Islands, in the southeastern Queen Charlotte Islands, Canada, contains 20 families, 33 genera, 61 species, 1 subspecies, and 2 varieties. Specifically on Burnaby—18 families, 28 genera, 44 species, 1 subspecies, and 2 varieties; on Hotspring—16 families, 21 genera, and 33 species; on Huxley—16 families, 18 genera, 32 species, and 1 subspecies; on Ramsay—17 families, 24 genera, 43 species, 1 subspecies, and 1 variety. Thirty-seven taxa (57.8%) of the total 64 taxa present are boreal in distribution. Thirteen taxa (20.3%) are western North American and amphi-Pacific elements. Other distribution patterns: 3 are cosmopolitan; 1 is disjunct-montane and arctic-alpine; 4 are circumtemperate; and 5 are temperate disjunct.

Introduction

The Queen Charlotte Islands (Haida Gwaii, including Gwaii Haanas National Park Reserve) lie in the Pacific Ocean 100 km west of the mainland coast of British Columbia and extend from 51° 54'– 54° 13' N to 130° 58'–133° 06'W. The landscape of the islands is the product of tectonic uplift and of glacial and fluvial erosion and deposition. During the major Pleistocene glaciation, the islands supported mountain ice caps and a network of valley and piedmont glaciers, independent of the Cordilleran ice sheet (Clague 1989). The lack of glaciation explains the occurrence of endemic and disjunct species in the islands (Schofield 1989). The islands consist of over 150 islands with many short inlets. The major islands are Graham (largest and most populous) and Moresby (Figure 1).

Schofield (1989) mentioned the occurrence of 136 species of hepatics and 323 species of mosses in the entire Queen Charlotte Islands. Among these, five are endemic species and seven are disjunct. He also commented that the luxurious growth of byrophytes is caused by the hyperoceanic climate that provides moisture and mild temperature, the great diversity of substrates, and the geographical position in relation to a richness of floristic sources.

Several papers have dealt with bryophytes in the Queen Charlotte Islands (Glime and Hong 1997, Hong 1999, Hong and Glime 1997, Hong et al. 1991, 1992, 1994, Peck et al. 1995, Persson 1958, Schofield 1968a, 1968b, 1976, 1989, Schuster and Schofield 1982). All these papers dealt with fragmental collection sites, mainly listing occurring taxa in the limited area, but none has compared hepatic flora and floristic affinities among the neighboring islands.

This study aims to determine (1) the number of occurrence of hepatics in each island; (2) the distributional categories for each species; and (3) similarities and dissimilarities for hepatic flora in four islands in the Queen Charlotte Islands.

Study Area

Burnaby, Hotspring, Huxley, and Ramsay Islands are located between 52°19'–52° 39' N and 131°14'–131° 27' W (Figure 1). These islands are faced on the east by Hecate Strait and on the west by Moresby Island through Perez Sound (Hotspring, Huxley, and Ramsay) and narrow Burnaby Strait (Burnaby) (Figure 1).

Generally moist air moves from the Pacific Ocean and it is forced to rise over the rugged westerly-running Queen Charlotte Mountain Ranges, then the air rises and cools, and much of the moisture condenses and falls as precipitation (always in the form of rain). The southern end of the islands is more exposed to the influence of North Pacific High and causes less precipitation by weak and infrequent storms. However, in the north and central parts of the islands are more exposed to Aleutian Low and bring more precipitation by frequent and often severe storms moving from the open Pacific. The nearest weather stations are Sewell Inlet in the north and Cape St.

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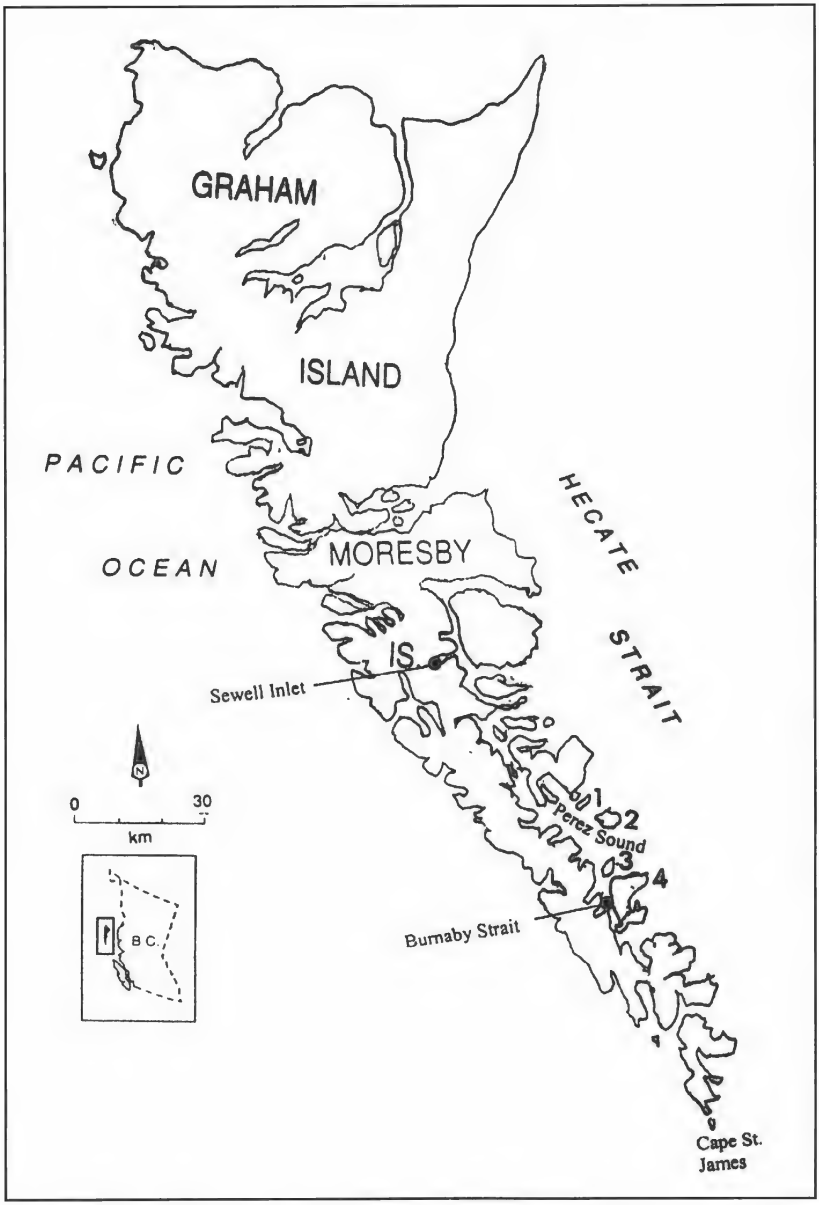

Figure 1. The study site consisted of four neighboring islands in the Queen Charlotte Islands. 1. Hotspring Island. 2. Ramsay Island. 3. Huxley Island. 4. Burnaby Island.

James in the south, both within 50 km of these islands (Table 1).

On the islands, dominant trees are western red cedar (*Thuja plicata),* western hemlock *(Tsuga heterophylla),* Sitka spruce (*Picea sitchensis*), and red alder (*Alnus rubra).* The forest floor is covered luxuriantly with bryophytes; occasionally Alaskan blueberry (*Vaccinium alaskaense*),

TABLE 1. Climate data from weather stations at Sewell Inlet and Cape St. James, Queen Charlotte Islands (Seel et al. 1990).

	Sewell Inlet	Cape St. James
Mean annual temperature (°C)	7.6	8.4
Mean January temperature (°C)	1.1	3.9
Mean August temperature (°C)	15.1	13.8
Mean annual precipitation (cm)	416.8	153.1

red huckleberry (*Vaccinium parvifolium*), and deer fern (*Blechnum spicant*) also occur. Especially abundant bryophytes are *Dicranum scoparium*, *Hylocomium splendens*, *Kindbergia oregana*, *Rhizomnium glabrescens*, and *Rhytidiadelphus loreus*. On tree bark, *Antitrichia curtipendula, Cephalozia bicuspidata, C. lunulifolia, Diplophyllum albicans, Frullania nisquallensis, Isothecium stoloniferum,* and *Scapania bolanderi* are abundant.

Methods

I traveled to the islands every summer from 1991 to 1999 and collected over 1,700 specimens. Collected specimens were returned to the laboratory and air-dried.

Voucher specimens have been deposited at the University of Great Falls, Montana (CGF), with available duplicates in the herbarium of Gwaii Haanas National Park Reserve, Queen Charlotte City, B.C., and the University of Cincinnati (CINN). In general, nomenclature follows Stotler and Crandall-Stotler (1977) and Grolle and Long (2000).

Results

Sixty-four taxa of hepatics were found on Burnaby, Hotspring, Huxley, and Ramsay Islands, including 20 families, 33 genera, 61 species, 1 subspecies, and 2 varieties. Burnaby Island with 28 genera, 44 species, 1 subspecies, and 1 variety. Hotspring and Huxley Islands had 21 and 18 genera and each with a total of 33 taxa.

The hepatic flora of the islands contained numerous common species and few rare species (Table 2). The following seventeen species occurred in all islands: *Bazzania flaccida, Blepharostoma trichophyllum, Calypogeia suecica, Cephalozia bicuspidata, C. lunulifolia, Diplophyllum albicans, Frullania nisquallensis, Lepidozia reptans, Lophocolea bidentata, Lophozia incisa, Metzgeria conjugata, Plagiochila porelloides, Porella navicularis, Radula bolanderi, Riccardia latifrons, Scapania bolanderi,* and *S. umbrosa.* Among these, the most common were *Scapania bolanderi* (274 specimens/collections), *Diplophyllum albicans* (122 specimens), *Bazzania flaccida* (107 specimens), *Cephalozia bicuspidata* (93 specimens), *Frullania nisquallensis* (88 specimens), and *Blepharostoma trichophyllum* (84 specimens). Nineteen taxa including 18 species and 1 variety, were found on only two islands (Table 2).

Discussion

Burnaby Island, due to its largest size and great diversity of substrates, was the most diverse collection site and Hotspring and Huxley Islands, due to their smaller size and less diversity of substrates, were the least diverse collection sites.

The known hepatic flora of Burnaby, Hotspring, Huxley, and Ramsay Islands represents nine different distributional elements (Tables 2 and 3). The presence of 10 western North American endemic and 3 Amphi-Pacific taxa represents 21.7% of the entire hepatic flora of the Burnaby Island (total 47 taxa) compared with 17.6% of the neighboring Huxley Island (total 33 taxa), 19% of Ramsay Island (total 45 taxa) and 24.1% of Thermal Meadow of Hotspring Island (total 33 taxa). The world distribution categories follow those given in Belland et al., Belland and Schofield (1992, 1994) and Hong (1999).

Cosmopolitan elements (three taxa, 4.7%). Species in the islands that show a cosmopolitan distribution include *Aneura pinguis, Riccardia multifida,* and *R. palmata.*

Circumboreal elements (30 taxa, 46.9%). Almost 60% of the hepatics of the islands belong to the boreal elements (57.8%). Such high percentage of boreal elements is similar to those of Belland et al. (68.1%; 1992), Bellland and Schofield (64.9%; 1994) in eastern Canada, and Hong (58.9%; 1999) in the Queen Charlotte Islands. The species in this category are widespread throughout the Northern Hemisphere within the boreal biomes. Representative taxa in the islands are *Barbilophozia hatcheri, Bazzania flaccida, Blepharostoma trichophyllum, Cephalozia lunulifolia, Lepidozia reptans, Lophozia incisa,*

TABLE 2. Known hepatics, the number of collections in which they occur, and their floristic affinities on Burnaby, Hotspring, Huxley, and Ramsay Islands. Taxa are listed alphabetically.

Taxon	Burnaby	Hotspring	Huxley	Ramsay	Affinity
Aneura pinguis	2			1	cosmopolitan
Apometzgeria pubescens				1	boreal disjunct
Barbilophozia hatcheri		3			circumboreal
Bazzania ambigua	1				western N. American
Bazzania flaccida	41	22	2	42	circumboreal
Bazzania tricrenata				5	circumboreal
Blepharostoma trichophyllum	19	12	7	28	circumboreal
Calypogeia azurea	2	5		4	circumboreal
Calypogeia integristipula	3		1		circumboreal
Calypogeia muelleriana	1			1	temperate disjunct
Calypogeia neesiana				1	circumboreal
Calypogeia sphagnicola	2			1	circumboreal
Calypogeia suecica	9	13	14	11	boreal disjunct
Cephalozia bicuspidata	28	9	27	54	circumtemperate
Cephalozia leucantha	6		17	7	circumboreal
Cephalozia lunulifolia	10	15	6	20	circumboreal
Cephalozia macounii	2	4		3	circumboreal
Cephaloziella divaricata	12				circumboreal
Chiloscyphus polyanthos			2		circumtemperate
Conocephalum conicum	16		10	7	circumboreal
Diplophyllum albicans	63	2	16	41	circumboreal
Diplophyllum plicatum	7	2		6	amphi-Pacific
Douinia ovata	1	1			temperate disjunct
Frullania californica		2			western N. American
Frullania franciscana	1	5	2	4	western N. American
Frullania nisquallensis	20	30	24	14	western N. American
Geocalyx graveolens		1		2	boreal disjunct
Gyrothyra underwoodiana				8	western N.American
Herbertus aduncus	10				temperate disjunct
Jungermannia leiantha				1	circumboreal
Jungermannia obovata	1				disjunct montane
Kurzia sylvatica	4			4	temperate disjunct
Leiocolea bantriensis			1		circumboreal
Lepidozia reptans	11	17	6	18	circumboreal
Lophocolea bidentata	2	3	1	2	temperate disjunct
Lophozia incisa	4	1	13	12	circumboreal
Lophozia longiflora		1	1		circumboreal
Lophozia ventricosa		2			circumboreal
Marsupella emarginata	1				circumboreal
Metzgeria conjugata	14	1	13	12	circumboreal
Moeckia hibernica				5	boreal disjunct
Mylia taylori	7	1		17	boreal disjunct
Odontoschisma denudatum	1	1			circumboreal
Pellia endiviifolia	1		3	3	circumboreal

Continued, next page

TABLE 2. Continued

Taxon	Burnaby	Hotspring	Huxley	Ramsay	Affinity
Pellia epiphylla	8		2	9	circumtemperate
Pellia neesiana	1			1	circumtemperate
Plagiochila asplenioides	1	1		2	circumboreal
Plagiochila porelloides	9	5	5	2	circumboreal
Plagiochila satoi		1	1	1	amphi-Pacific
Plagiochila satoi var. *magnum*	1				western N. American
Plagiochila schofieldiana	6				western N. American
Porella cordaena		3			boreal disjunct
Porella navicularis	11	17	20	9	western N. American
Radula bolanderi	4	5	7	4	western N. American
Radula obtusiloba subsp. *polyclada*	6		1	18	western N. American
Riccardia latifrons	12	3	15	16	circumboreal
Riccardia multifida	6		2	1	cosmopolitan
Riccardia palmata	8		8	14	cosmopolitan
Scapania bolanderi	93	32	53	96	amphi-Pacific
Scapania paludosa	2		1	1	arctic alpine
Scapania umbrosa	6	2	12	11	circumboreal
Scapania undulata	11		2	8	circumborea
Scapania undulata var. *oakesii*	1			4	boreal disjunct
Tritomaria exsecta	1				circumboreal
Total taxa	47	33	33	45	

TABLE 3. The floristic affinities of the hepatics of Burnaby, Hotspring, Huxley, and Ramsay Islands.

Elements	Number of hepatics (%)
Cosmopolitan	3 (4.7)
Circumboreal	30 (46.9)
Boreal disjunct	7 (10.9)
Circumtemperate	4 (6.2)
Temperate disjunct	5 (7.8)
Disjunct montane	1 (1.6)
Arctic alpine	1 (1.6)
Amphi-Pacific	3 (4.7)
Western North American	10 (15.6)
Total	64 (100.0)

Plagiochila asplenioides, Scapania umbrosa, and *S. undulata.*

Boreal disjunct elements (seven taxa, 10.9%). The species of this group have major gaps in their world distribution. These taxa existed on the islands through all of the recent glaciations. Representative taxa are *Apometzgeria pubescens, Calaypogeia suecica, Geocalyx graveolens, Moerckia hibernica, Mylia taylori, Porella cordaena,* and *Scapania undulata* var. *oakesii.*

Circumtemperate elements (four taxa, 6.2%). The taxa of this group are widely distributed in the temperate forests of the Northern Hemisphere including Europe, Asia, and eastern and western North America. Representatives are *Cephalozia bicuspidata, Chiloscyphus polyanthos, Pellia epiphylla,* and *Pellia neesiana.*

Temperate disjunct elements (five taxa, 7.8%). The taxa of this group occur in the same region as the group of circumtemperate element, however, they are absent from one or two of the above regions. The species could have survived the Pleistocene glaciation. Representatives are *Calypogeia muelleriana, Douinia ovata, Herbertus aduncus, Kurzia sylvatica,* and *Lophocolea bidentata.*

Disjunct montane (one taxon, 1.6%). Only *Jungermannia obovata* belongs to this element.

Arctic-alpine element (one taxon, 1.6%). This taxon, *Scapania paludosa* is restricted to Arctic and alpine areas. The low percentage of Arctic-

alpine element is due to lack of fen which supports the richest representation of this element, and its low elevation in the islands (all are < 300 m, except Burnaby Island), in contrast to those of Belland et al. (8.7%; 1992), Belland and Schofield (4.1%; 1994), and Hong (3.1%;1999). All these areas are rich in fens and elevations are higher than those of the four islands.

Amphi-Pacific elements (three taxa, 4.7%). The taxa of this group occur in the Northern Pacific coast of Asia (from Kamchatka to the northern tip of the Philippines, including the southeastern area of China, Formosa, the southern part of Korea, and Japan) and North America (from Alaska to California, including the southwestern part of Yukon, Idaho, and the western part of Montana). Representatives are *Diplophyllum plicatum, Plagiochila satoi* [So and Grolle (2000) treated as synonym of *P. porelloides*], and *Scapania bolanderi.* The percentage represented by this element is similar to those in the Vladimir Krajina Ecological Reserve, on Graham Island (Hong 1999).

Western North American endemic elements (10 taxa, 15.6%). This group is restricted to the western part of North America, and includes *Bazzania ambigua, Frullania californica, F. franciscana, F. nisquallensis, Gyrothyra underwoodiana, Plagiochila satoi* var. *magnum, P. schofieldiana, Porella navicularis, Radula bolanderi,* and *R. obtusiloba* subsp. *polyclada.* The percentage represented by this element is similar to those of Hong (1999) for Graham Island.

The basic hepatic flora in boreal areas in North America, Asia, and Europe is the same. The strong resemblance between eastern Canada boreal hepatic communities (Belland et al. 1992, Belland and Schofield 1994) and these four islands and Graham Island (Hong 1999) is due to their similar Northern boreal location (between 45° and 50° N), the influence of similar hyperoceanic climates that favor bryophyte growth, their reliability to construct natural distribution patterns, and lack of human disturbances (all areas are strictly controlled by Canadian Government).

Acknowledgements

The author thanks Drs. M. Easton, F. Gilliard, D. Olson, W. Furdell, A. Alt, Rev. J. Sikora, and Sister Benoit for their assistance. I am also grateful to Dr. D. Burles and Ecologist T. Golumbia, Gwaii Haanas National Park Reserve for permission to study the hepatic flora of these Islands. Finally I would like to express my sincere gratitude to Drs. P. Davidson, J. Harpel, and D. Wagner.

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Received 22 October 2001
Accepted for publication 8 May 2002

Marianne Elliott, Robert L. Edmonds, and **Scott Mayer,** College of Forest Resources, University of Washington, Seattle, Washington 98195

Role of Fungal Diseases in Decline of Pacific Madrone

Abstract

There is concern over the health of Pacific madrone, a tree native to California, Oregon, Washington, and British Columbia. Declining trees have been reported in western Washington and British Columbia during the past 30 yr. The fungus *Nattrassia mangiferae* causes cankers and shoot blight and is associated with declining madrones. *Fusicoccum aesculi* causes branch dieback but is a secondary pathogen that attacks stressed trees. We found both fungi on declining madrone trees. More canker fungi were isolated within the first cm from the canker margin, and occurred more often on large diameter wood. *Nattrassia mangiferae* was found in 90% of samples from the margin of madrone cankers and is considered the primary pathogen. Trees that were heavily infected with canker fungi had less stored starch in the root burl. Starch content in the root burl of declining trees was significantly lower than in healthy trees. Pacific madrone decline has a similar pattern to other declines involving early successional species that establish after a disturbance, where mature trees are more severely affected. Fire was the major natural disturbance agent with madrone, but disease now appears to be replacing fire as the main disturbance agent responsible for killing aboveground plant parts. Unlike fire, disease decreases starch accumulation in the root burl, so that declining trees are less able to resprout after the aboveground portion of the tree is killed by disease.

Introduction

A decline in Pacific madrone (*Arbutus menziesii*) has been reported during the past 30 yr in the Pacific Northwest (Davison 1972, Bressette 1995), and there is great concern about the health of this species that is native to the western U.S. and British Columbia. The problem was first seen in urban areas, but declining trees are also found in natural forests. All ages and sizes of madrones are affected, with larger, older madrones having the most mortality. The major cause appears to be a canker disease caused by the fungus *Nattrassia mangiferae* (Deuteromycota) (Davison 1972, Hunt et al. 1992, Bressette 1995) (Figure 1). The first cases of cankers and declining madrones in Washington State were reported after a hot summer in 1967 followed by an unusually cold winter in 1969 (Davison 1972).

Nattrassia mangiferae may be an introduced fungus since it first appeared in the 1960s in Washington, and probably spread to madrone from Persian walnut in California, where it causes a wilt disease (Paxton and Wilson 1965). Low disease resistance in madrone, severe weather conditions, and the practice of fire suppression in the 20th century may have allowed this typically weak pathogen to become a serious problem on Pacific

Figure 1. Declining madrone trees and associated cankers. The large, callusing cankers are typical of *Nattrassia mangiferae* infections.

[1] Author to whom correspondence should be addressed. E-mail: melliott@u.washington.edu

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madrone. Greater weakening of trees through defoliation is caused by the opportunistic pathogen *Fusicoccum aesculi* (Deuteromycota).

A fungus similar to *Nattrassia mangiferae* was first reported in the U.S. on Persian walnut in California in 1947 (Wilson 1947) and named *Exosporina fawcetti*, later renamed to *Hendersonula toruloidea*. *Hendersonula toruloidea* was later placed in its own genus, *Nattrassia*, of which *N. mangiferae* is the type species (Sutton and Dyko 1983). The fungus was originally found on plum, apricot, and apple (Nattrass 1933) and has been reported from many tropical and sub-tropical countries where it is a weak pathogen that colonizes injured wood (Paxton and Wilson 1965, English et al. 1974, Sutton and Dyko 1989). Heat injury to the bark is required in most cases. Hot, dry weather encourages the development of disease symptoms (Calavan and Wallace 1954, Davison 1972, Pandey et al. 1981, Jayasingh and Silva 1994, Msikita et al. 1997). *Nattrassia mangiferae* is especially destructive on thin-barked trees that grow where summer heat is intense. In addition to being a plant pathogen, the fungus causes skin disease on humans and other animals (Sigler et al. 1997). In both plant and animal hosts, infection by *N. mangiferae* is not normally a problem unless the host is under some type of stress.

On Pacific madrone, *N. mangiferae* infects the phloem and vascular cambium and causes shoot blight. Infection courts are generally created by mechanical injury or sunscald. Shaded trunks of madrone trees develop a thick layer of bark that is thought to protect the tree from fungal infection (Bressette 1995). Heat-injured bark and wounds become infected with conidia of *N. mangiferae*. Cankers first appear as an area of purplish to black bark discoloration. The bark peels off revealing longitudinally cracked wood and dark masses of asexual fungal spores (Figure 2). Conidia (arthrospores) are present all year in the dead wood of the canker and are carried by the wind to infect new hosts (Hunt et al. 1992). Inner bark and sapwood in the area around the cankers is discolored brown in contrast to healthy tissue, which is white or pale green.

Fusicoccum aesculi (*Botryosphaeria dothidea* (Ascomycota), teleomorph) has also been associated with declining madrone trees, and a large proportion of mature trees in northern California are dying from cankers and branch dieback caused by this fungus (McDonald and Tappeiner 1991). On Pacific madrone, *F. aesculi* causes branch dieback where the limbs and twigs appear burned (Adams and Kosta 1993, Adams et al. 1999). Tiny black pycnidia are visible on the leaves and twigs. On many hosts this fungus can be present in the wood without causing disease, growing saprophytically on dead tissue or remaining latent until the water content of the wood falls below a critical level. Symptoms develop when the host becomes drought-stressed (Houston 1984, Pusey 1989, Boyer 1995).

When madrone branches and terminal buds are killed by fungi, they are unable to produce more foliage. The tree resprouts from dormant buds on the stem or root burl and grows new shoots to increase the amount of foliage in a manner similar to that occurring after a fire (USDA Forest Service 2002). These new shoots are often attacked and killed by *N. mangiferae*.

Aging madrone trees develop a large root burl with a spreading root system, which allows the trees to resprout when damaged by fire or disease. Dormant vegetative buds used in resprouting are located just above the root collar and grow rapidly when released. Trees that have lost much of their crowns from canker fungi and dieback will resprout if these vegetative buds are not damaged by cankers. Below the root collar madrones have a root burl, or lignotuber, which contains stored starch. Resprouting species allocate more carbon to storage in the root burl than do species that reproduce primarily by seed (Bell and Ojeda, 1999). Trees 50-60 yr old have a well-developed root burl with deep, spreading lateral roots (McDonald and Tappeiner 1991). These large trees are susceptible to heart rot, which makes them desirable for cavity-nesting birds (Raphael 1987).

Dominant and codominant individuals of early successional tree species that establish after a disturbance tend to show decline symptoms before younger members of the stand. This phenomenon is called cohort senescence (Gerrish 1993, Mueller-Dombois 1993) and is a natural part of the species life cycle. Large, old madrones are more susceptible to decline because madrone is an early successional species adapted to frequent fires (McDonald and Tappeiner 1991, USDA Forest Service 2002). Madrones have a growth rather than a defense strategy, which allows young plant parts, such as resprouts or seedlings, to be

Figure 2. Arthrospores and conidia of *Nattrassia mangiferae* taken from a madrone canker. 400x.

competitive in early stages of stand development (Loehle 1987). When these trees approach maturity and senescence, growth slows due to a decreased ratio of photosynthesis to respiration caused by the higher proportion of support tissue relative to leaves. Rapid growth can no longer be used as a defense and the tree is more susceptible to attack by pathogens. As the crown becomes defoliated by pathogens, the amount of photosynthesis relative to respiration decreases even more and opportunistic pathogens, such as *Armillaria*, attack the weakened tree. Water stress on the whole tree increases as the roots become compromised, further weakening the tree. After a certain point, the tree does not have enough carbon in reserve to defend against pathogens and re-grow damaged parts. This process, where the tree has low defenses, is compromised by a short-term stress. The

tree dies due to the activity of secondary organisms in a process called a decline spiral (Manion 1981). Vigorous trees can escape and regrow damaged parts, but trees with low carbon reserves often die.

The objectives of our research were to determine: (1) the role of canker fungi in madrone decline in the Puget Sound area, (2) the fungal composition of cankers and the influence of branch size and distance from the canker margin, and (3) the effects of *Nattrassia* and *Fusicoccum* on starch reserves in the root burl.

Methods

Study Sites

The sites chosen for this research were in King County, Washington. All sites were influenced by urbanization and included city parks and other public and private property. The sites ranged from steep, exposed bluffs to flat, protected areas. Soils were generally sandy, but in some areas compacted or waterlogged.

Fungal Composition of Madrone Cankers

Madrone trees growing on four sites in King County, Washington were sampled during the summer of 1997. These sites were Discovery Park, Seward Park, Maury Island, and the University of Washington campus in Seattle. Samples were taken from (1) newly forming cankers without a callus ridge and (2) older cankers with callus and possibly decay on both small (<20 cm) and large diameter stems and branches. Five cankers were sampled from each type. Four wood chips from the phloem, cambium and first few rings of sapwood were removed with a chisel at distances of 0, 0.5, 1, 2, 4, and 8 cm above and below the canker margin. If the branch was dead above the canker, all samples were taken below the canker in living tissue. The wood chips were surface sterilized in a dilute solution of sodium hypochlorite and rinsed in deionized water. They were placed in petri dishes containing 2% malt extract agar and incubated at 25°C for one week. The number of wood chips containing the canker fungi *N. mangiferae* and *F. aesculi* were counted. Other fungi, including yeasts, and bacteria were noted. Isolates of *N. mangiferae* from Seattle were compared to two isolates from the culture collection at the University of Alberta Microfungus Collection and Herbarium (isolates UAMH 6799 and UAMH 6800). *Nattrassia mangiferae* isolates from madrone were also compared with descriptions in the literature (Wilson 1949, Sigler and Carmichael 1976, Sutton and Dyko 1989). Fungi thought to be *F. aesculi* were isolated and compared with descriptions in the literature (English et al. 1974, Pennycook and Samuels 1985, Rayachhetry et al.1996, Gardner 1997). It was not possible to obtain a culture of this fungus from a culture collection.

Two-way ANOVA was used to compare isolation frequencies of canker fungi in the different canker types on large and small diameter wood. Isolation frequencies of the fungi at different distances from the canker margin were also compared. The Tukey multiple comparison test was used to examine means which were significantly different at the P=0.05 level (Neter et al. 1990).

Koch's postulates were tested with a randomly selected isolate of *N. mangiferae* on 24 two-year old madrone seedlings grown in 24 cm diameter pots containing unfertilized vermiculite and peat. They were kept in a glass shelter under outdoor conditions of light and temperature at the University of Washington. A 1 cm cut was made into the sapwood about halfway up the stem of each plant. Four of the plants served as controls, with a sterile toothpick inserted into the wound. The other plants were inoculated with toothpicks colonized by *N. mangiferae*. After each plant was treated, the wound was wrapped in parafilm. The toothpicks and parafilm were removed after 2 wk. Lesions were later sampled and *N. mangiferae* was re-isolated from inoculated plants.

Effects of Disease on Stored Starch

Two hundred fifty-eight madrone trees growing on six sites in King County were surveyed during summer 1997. The sites were three Seattle city parks (Magnolia Bluffs, Seward, and Lincoln), the University of Washington campus, the Crossroads area of Bellevue, and the Northgate area of Seattle. All sites were in urban areas and ranged from lightly used areas with the madrones growing mixed with other tree species and native vegetation in greenbelts to heavily disturbed, where the madrones were part of a landscape that included lawn, ornamental plantings, or concrete. Information was collected on madrone health including amount of cankering and defoliation from branch dieback.

Percent foliage (%FOL) was calculated from the following formula to get a more realistic measurement of the tree's photosynthetic ability

$$\%FOL = [LCR - (LCR * DEAD)] * 100$$

where LCR = live crown ratio and DEAD = fraction of the crown with branch dieback. On heavily diseased trees, the base of the live crown was estimated to be where live foliage would begin if the tree was healthy based on branching patterns. Diameter (dbh) was also measured. The amount of cankering on the main stem and branches was determined by classifying trees into three groups based on the number of cankers. Group 1 trees contained 0 - 5 stem cankers, group 2, 5 –15 cankers, and group 3, >15 cankers.

A subset of 55 trees from these sites was used for starch analysis in February 1997. They were classified using crown architecture as a measurement of physiological age with a seven stage Architecture Based Classification (ABC) (Gatsuk et al.1980, Mayer 1998) (Figure 3). Stored starch in the lignotuber represented an objective index of tree vigor and a measurement of the resources available after respiration.

In addition to these trees, a second starch sampling was performed on a group of mature madrone trees of similar age and size at the Lincoln Park site in February, 2000. They were separated into groups of healthy (≥50% foliage) and unhealthy (<50% foliage) trees.

Samples from each madrone tree were taken with an increment borer at four locations around the root burl. The first 1 cm of sapwood inside the phloem was used for each sample. The samples were placed on dry ice immediately after removal

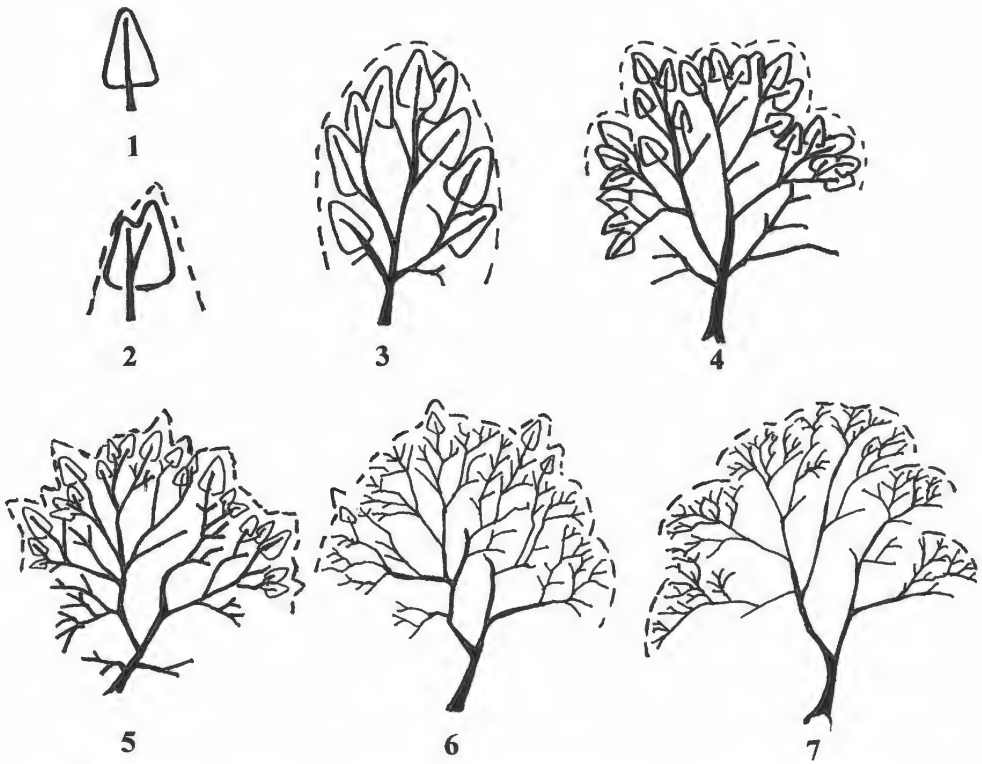

Figure 3. Architecture Based Crown classification (ABC) for Pacific madrone representing physiological age. Stage 1 is the juvenile stage with one central axis. There is increased shoot growth in stages 2 – 5, decreasing as the trees grow in size. As the shoot length decreases, the number of shoots increases. The trees develop a flatter, less dense canopy concentrated at the top of the crown in later stages (6 and 7).

from the tree and then kept at –20°C until analysis. They were dried for 48 hr at 70°C, then ground to a powder for starch analysis. We assumed that starch was stored in the ray cells and inter-ray xylem, and would be present throughout the whole core, since Pacific madrone is a resprouting species (Bell and Ojeda 1999). Thus, the diameter of the tree was irrelevant.

Stored starch was determined using methods modified from Haissig and Dickson (1979) and Kolb and McCormick (1991). Fifty mg of the ground sample was extracted three times with 80% ethanol. The pellet was dried overnight at 70°C. The next day, it was resuspended in acetate buffer at pH 4.5, gelled for 15 min in boiling water, and cooled in an ice bath. Starch was converted to glucose by adding 1 ml of amyloglucosidase (15 units/ml) and incubating for 24 hr at 50°C. After incubation, the samples were removed from the oven and 0.1 ml of sample was added to a 0.4 ml buffer. Five ml of enzyme color reagent (Sigma kit #510) was added to each tube and incubated for 30 min in a 37°C water bath. Absorbance for each sample was read in a Perkin-Elmer 55E spectrophotometer at 450 nm. The amount of glucose in the sample was calculated from a glucose standard regression curve.

The data from the Lincoln Park site were analyzed by t-tests on groups of healthy (percent foliage ≥50%) and unhealthy (percent foliage <50%) trees with respect to starch content, dbh, live crown ratio, percent dead branches, and percent foliage. Stored starch was expressed as mg glucose/g sample. The Mann-Whitney U test (Neter et al 1990) was used to determine the differences in the frequency of stem cankers in healthy and unhealthy trees.

Relationships between ABC crown class and other variables and the number of stem cankers and other variables were examined using one-way ANOVA on the data from the other sites. The Tukey multiple comparison test was used to examine means that were significantly different at the P=0.05 level (Neter et al. 1990). Data were analyzed using SPSS v. 10.0.

Results

Fungal Composition of Madrone Cankers

Nattrassia mangiferae, Fusicoccum aesculi, and *Trichoderma* spp. occurred the most frequently in culture. *Nattrassia mangiferae* was found more often than any other species in all cases, and was found in samples from the canker margin 90% of the time. The fungi *Fusicoccum aesculi* and *Trichoderma* spp. were isolated from about 10% of the samples. In some cases, growth of *Trichoderma* suppressed that of *Nattrassia.*

Other fungi present in smaller numbers were *Penicillium* spp., *Fusarium* spp., and *Aspergillus* spp., and yeasts. Bacteria were also present.

Microscopic examination showed no morphological difference between isolates of *N. mangiferae* from Pacific madrone cankers in Seattle and isolates from madrone cankers in British Columbia that were in the University of Alberta culture collection. The main identifying feature of *N. mangiferae* is the production of pigmented arthrospores (Figure 2), which distinguishes it from *F. aesculi*. Both of these fungi produce dark mycelia in culture. The isolates from Pacific madrone in Seattle also conform to the descriptions of *N. mangiferae* in the literature (Sutton and Dyko 1989). In the test of Koch's postulates, all the trees inoculated with *N. mangiferae* developed cankers that contained the fungus. These cankers were growing vertically along the stem and were smooth and black, similar to newly developing cankers found on stressed madrone trees in the field.

The number of organisms isolated decreased with distance from the canker margin. In some samples, especially those taken farthest from the canker margin, no fungi were isolated. The number of samples containing *N. mangiferae* declined significantly ($P < 0.001$) with distance from the canker margin. There was a ~50% decrease between 0 and 0.5 cm (Figure 4). The fungus was found in only 21% of the samples at the distance of 8 cm.

Differences between canker types were significant for *N. mangiferae*, with the fungus found most often in actively growing cankers on large diameter wood (Figure 5) ($P = 0.03$). *Nattrassia mangiferae* was found least often in cankers on small-diameter branches. There was no significant difference in the amount of *N. mangiferae* found in new and old cankers, and in cankers on stems vs. branches.

Fusicoccum aesculi did not occur in as many samples as *N. mangiferae*, but was found most frequently in cankers on small-diameter branches

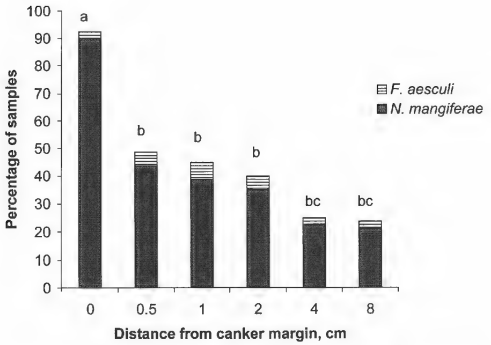

Figure 4. Isolation frequency of the canker fungi *Nattrassia mangiferae* and *Fusicoccum aesculi* from Pacific madrone cankers. Average percentage of isolations out of 20 attempted for distance from the canker margin. The highest proportion of isolations was made up to 1 cm from the canker margin. No organisms were isolated from many of the samples at distances greater than 2 cm from the canker margin. There were significant differences in the amount of *Nattrassia mangiferae* related to distance from the canker margin ($P<0.01$). Letters above each bar indicate significant differences in the amount of *Nattrassia* isolated. There were no significant differences in the amount of *Fusicoccum* isolated.

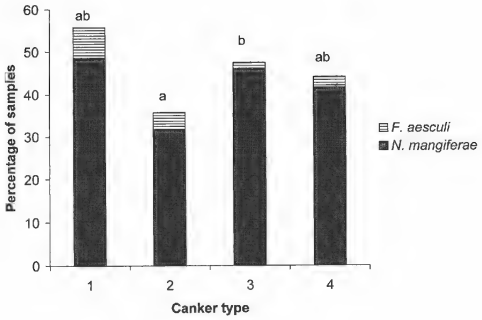

Figure 5. Isolation frequency of the canker fungi *Nattrassia mangiferae* and *Fusicoccum aesculi* from Pacific madrone cankers. Average percentage of isolations out of 20 attempted for each canker type. The canker types sampled were the following: 1 = new cankers on branches < 20 cm diameter, 2 = old callusing cankers on branches, 3 = new cankers on stems and branches > 20 cm diameter, and 4 = old callusing cankers on stems. Five cankers were sampled for each type, with four samples taken from each location. There were significant differences in the amount of *Nattrassia mangiferae* related to each canker type ($P<0.05$).

(Figure 5). It was found most often at the distance of 1 cm from the margin, as opposed to *N. mangiferae*, which occurred most often at the canker margin (Figure 4). It occurred in the same canker as *Nattrassia* on several samples taken from canker margins, as noted by English et al. (1974) on almond trees.

There were no significant differences among the canker types and distances from the canker margin for *Trichoderma* spp., however, more *Trichoderma* spp. was observed in older cankers. These cankers tended to have less *N. mangiferae* than newer cankers. There was no relationship between the amount of *Trichoderma* spp. and *F. aesculi* in the cankers.

Effects of Disease on Stored Starch

Large diameter trees tended to have less live foliage in the crown and more stem cankers than small diameter trees. The amount of branch dieback in the crown increased with the number of cankers on the main stem (Table 1).

Stored starch was highest in ABC crown classes 3 through 6 and lowest in young trees (crown classes 1 and 2) and in the oldest trees (crown class 7) (Table 2). Mean diameter of the trees in each group increased and the percentage of foliage decreased, with a large decrease in foliage between crown classes 6 and 7. There was a similar decrease in starch content between these two groups, suggesting that >50% defoliation affects the amount of stored starch in mature trees.

In a selected group of large diameter trees (mean dbh 68 cm) at the Lincoln Park site, healthy trees (≥50% foliage) had fewer stem cankers than unhealthy trees (< 50% foliage) (Figure 6). Healthy mature madrones had more stored starch than

TABLE 1. Number of *Nattrassia* cankers on the main stem and large branches of Pacific madrone relative to mean stem dbh and branch dieback. Standard error in parentheses. Different letters within columns indicate significant differences. ($P < 0.05$).

Number of cankers/tree (number of trees)	dbh(cm)	Branch dieback (%)
0 – 5 (86)	38.2^{a} (2.3)	16.1^{a} (2.5)
5 – 15 (32)	46.3^{b} (2.6)	29.9^{b} (3.4)
>15 (25)	48.9^{b} (1.8)	54.2^{c} (2.7)

TABLE 2. Summary of data for madrones in each ABC (Architecture Based Crown Class). Stored starch is expressed in terms of mg glucose/g sample. Numbers followed by a different letter in each row are significantly different ($P < 0.05$).

ABC	1	2	3	4	5	6	7
Number of trees	2	7	5	8	13	18	7
dbh (cm)	5.0[a]	5.4[a]	32.2[ab]	40.4[b]	39.6[b]	59.3[b]	59.0[b]
% dead	0[a]	0[a]	2.0[a]	2.5[a]	10.5[a]	17.1[ab]	51.7[b]
% foliage	100[a]	100[a]	77.7[ab]	73.1[ab]	40.4[bc]	41.9[bc]	12.2[c]
Starch (mg/g)	49.3[ab]	57.7[ab]	77.9[c]	65.5[abc]	65.7[abc]	68.4[bc]	46.7[a]

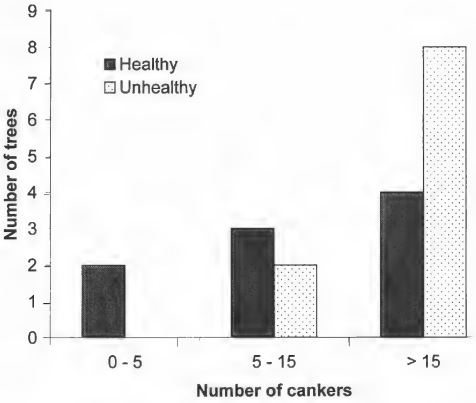

Figure 6. Number of stem cankers on a selected group of large diameter trees (mean dbh 68 cm). Healthy trees (> 50% foliage) had fewer stem cankers than unhealthy trees (< 50% foliage) (P = 0.08, Mann-Whitney U test).

TABLE 3. Results of t-tests between healthy (≥50% foliage) and unhealthy (<50% foliage) on mature madrone trees at Lincoln Park, Seattle, Washington for dbh, live crown ratio (LCR), % crown dieback, % foliage, and stored starch. Standard error in parentheses.

	Healthy	Unhealthy	*P*
dbh (cm)	58.3 (22.5)	54.3 (15.7)	0.66
LCR	0.80 (0.04)	0.77 (0.26)	0.92
% crown dieback	27 (6)	78 (4)	<0.01
% foliage	50 (4)	13 (3)	<0.01
Stored starch (mg/g)	2.22 (1.04)	1.18 (0.70)	0.02

unhealthy trees (Table 3). Starch levels were generally lower in this group than those shown in Table 2 because the trees were sampled in February 2000 when the average temperature for November through February was 6.7°C. This was a warmer winter than 1997, when the first group of starch samples was taken, when the average temperature was 5.3°C (Western Regional Climate Center 2002). The higher temperature in 2000 may have resulted in more growth and less starch storage in Pacific madrones, since they are an evergreen species and can photosynthesize during the winter if conditions are favorable.

Discussion

Nattrassia mangiferae appears to be an introduced fungus and is causing considerable dieback and mortality in Pacific madrone in western Washington. Low disease resistance in madrone, severe weather conditions, and the practice of fire suppression in the 20th century may have made this typically weak pathogen a serious problem on Pacific madrone. Greater weakening of trees through defoliation is caused by the opportunistic pathogen *Fusicoccum aesculi*.

Without fire to destroy inoculum, disease can increase in a stand of Pacific madrones. Aboveground parts are killed by disease rather than fire. Infection by *N. mangiferae* and *F. aesculi* may also reduce fruit and seed production by killing fruit-producing twigs in the upper crown. Declining trees are less able to resprout after the aboveground portion of the tree is killed by disease since the root burl is depleted of starch. It appears that disease is replacing fire as the main disturbance agent responsible for killing aboveground plant parts.

Stored starch decreases with physiological age, reducing reserves to defend against disease and predisposing the trees to decline (Table 2). This trend was also seen in the group of mature madrones sampled at Lincoln Park and is similar to forest declines in which the dominant and codominant trees in a stand have the most severe decline symptoms (Manion, 1981, Gerrish 1993, Mueller-Dombois 1993). This pattern is common in species

that establish after a disturbance such as fire and are shade intolerant (Ogden et al. 1993). The critical diameter for open-grown or codominant madrones seems to be around 40 cm. A madrone tree that is >40 cm dbh is in balance between carbon production and demand. A stress that causes the tree to lose some of its foliage will decrease the ratio of photosynthetic to respiring area and cause the tree to begin to decline (Gerrish 1993, Ogden et al. 1993). Larger, older trees lack the resources to defend themselves against canker fungi by growth or defensive chemicals, both of which require carbon.

Defoliation as a result of the presence of canker fungi can add to the effects of age on a mature madrone tree. *Nattrassia mangiferae* cankers girdling the stem create water stress in the crown. Under these conditions, the opportunistic pathogen *Fusicoccum aesculi* becomes active and kills twigs and branches. A decline spiral (Manion 1981) is created when the trees have lost >50% of their canopy to branch dieback. Stored starch levels in mature trees drop significantly when compared to trees with less than 50% defoliation (Tables 2 and 3). Trees with >50% defoliation may have difficulty escaping the decline spiral without sufficient carbohydrates available for growth and defense because their photosynthetic ability is lessened. Changes in carbohydrate chemistry in defoliated madrones may also reduce their resistance to other pathogens, such as *Armillaria* (Garraway et al. 1991). Increased infection by *Armillaria* would create more water stress, further reducing tree defenses and increasing damage by canker fungi. A study of carbohydrate metabolism in declining madrones needs to be conducted to confirm this.

Small-diameter branches in the upper crown of madrone trees exhibit symptoms of dieback before large-diameter branches and the main stem. During drought periods small-diameter branches are the first to undergo water stress, causing *Fusicoccum aesculi* to become aggressive (Houston 1984, Boyer 1995). Additional water stress due to *N. mangiferae* cankers lower on the tree can also decrease the water supply to the upper branches. *Fusicoccum* was not isolated as often as *Nattrassia* from cankers in our study. *Fusicoccum* may cause more damage to madrones in California than in western Washington and British Columbia because of the drier climate there. In California, *Fusicoccum* produces wedge-shaped cankers on madrone (McDonald and Tappeiner 1991), but we did not observe these. However, all the declining trees had *Fusicoccum* dieback in the crown. We tended not to sample these branches and concentrated our sampling on typical *Nattrassia* cankers that occur more commonly on large diameter material. *Fusicoccum* could be more important than our sampling indicated. Although *Fusicoccum* may cause more damage on madrones in California, in western Washington and British Columbia *Nattrassia* is the primary canker pathogen on larger diameter material. *Trichoderma* is not known to be pathogenic and may be competing successfully for space and nutrients with *Nattrassia* in older cankers.

Acknowledgements

This research was supported by grants from Save Magnolia's Madrones and the City of Seattle Department of Neighborhoods. We thank L. Sigler for culture material and the Center for Urban Horticulture, University of Washington for potted plants.

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Received 11 February 2002
Accepted for publication 5 July 2002

Donald B. Zobel, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902 e-mail: zobeld@bcc.orst.edu

Ecosystem Use by Indigenous People in an Oregon Coastal Landscape

Abstract

Data regarding probable uses of biological materials by the indigenous people of the Salmon River-Cascade Head area of the Oregon coast were used to estimate the people's use of various ecosystems near villages. Of 308 uses identified, 256 were attributable to a given species; 124 species were identified. All local ecosystems were important sources of organisms for the people, with no apparent concentration of highly used species in any particular ecosystem. One species was cultivated, one domesticated, and five acquired by trade. Four major plant resources, camas, yew, hazel, and beargrass, are not known from the Cascade Head landscape, but may have been available from elsewhere in village territory. House construction without use of cedar planks, as indicated by ethnographic records, may have resulted from the paucity of western redcedar in the Salmon River lowlands. The scarcity of several widely used taxa near coastal village sites, especially western redcedar, may have limited the wealth of this indigenous population, even on the resource-rich Oregon coast.

Introduction

Indigenous people used resources primarily from the landscape in which they resided. The natural distribution of resources governed the pattern and richness of their lives. Determining where they obtained and how they used resources can help us understand where and how they lived, and how ecosystems have changed since Euro-American settlement.

Data about the use of plants and animals by indigenous Oregon coastal tribes are limited, but useful (Lyman 1991, Lindsay 1995). A few detailed interviews were recorded with persons born before Euro-American settlement. Archeological study has been rewarding, as bone, shell, and antler are preserved well within the shell-dominated middens (Lyman 1991, Hall 2001). Detailed study, however, is of limited extent even at the best-known Oregon sites. Beckham et al. (1982), Lyman (1991), Lindsay (1995), and Erlandson et al. (1998) have summarized information for numerous sites and tribes along the Oregon coast.

Understanding how a single local population used resources requires detail beyond that provided by the summaries, as differences in usage among tribes, villages, households, and times have been described (Barnett 1937, Newman 1959, Lyman 1991, Connolly 1992, Lindsay 1995). For this study, I combined information from anthropologists with local, detailed ecological data. I developed a list of organisms used by one subtribal group, the Salmon River people of the Tillamook, who resided near Cascade Head on the north-central Oregon Coast, in an area where information about historic and modern plant and animal species distribution is unusually complete. The list of taxa used was compared to historic and current species distribution in local and regional ecosystems. An estimate was made of the origin of each plant and animal used, based on ecosystem location relative to village sites and species' importance in each ecosystem. Thus, the relative usefulness to indigenous people of each ecosystem could be estimated. Local scarcity was identified for some widely used species. I suggest effects of and compensations for local scarcity of these important resource organisms.

Study Area

The region of study is in and near the Salmon River drainage, on the north central Oregon coast between Lincoln City and Neskowin, just north of 45°N latitude. It includes primarily the Cascade Head Scenic-Research Area and Cascade Head Experimental Forest of the USDA Forest Service, Siuslaw National Forest. I refer to this area as the Cascade Head landscape, named for the prominent headland bordering the Salmon River to the north. Forests, marshes, and grasslands in this area have been studied scientifically and distributions of vascular plants and vertebrates recorded in detail (Greene and Blinn 1991; unpublished species lists on file, Forestry Sciences Laboratory, USDA Forest Service, Corvallis, Oregon). The Salmon River estuary is less disturbed

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than most others in Oregon (Murray and Marrant 1983). The territory controlled by the Salmon River villages extended south several kilometers into the current location of Lincoln City and inland to the crest of the Coast Range (Beckham et al. 1982).

The Salmon River is small, draining 210 km^2. The Salmon River has 306 ha of estuarine habitat, including 223 ha salt marsh, 51 ha tideland, and 32 ha submerged land (Thompson and Snow 1974). There is evidence in the estuary of earthquake-induced subsidence and tsunami deposition, which covered Indian hearth areas about A.D. 1700 (Minor and Grant 1996). A sand spit blocking most of the estuary mouth supports dune forest and grassland, although there was probably less stable vegetation there before the introduction of European beachgrass (*Ammophila arenaria)* (Wiedemann 1984). A 69 ha grassland dominates the southwestern promontory of Cascade Head, just uphill from major village sites. Cascade Head also supports smaller grasslands above the ocean cliffs farther north. Little rocky shore can be reached on foot, but much is accessible by water. Steller's and California sea lions (*Eumetopias jubatus, Zalophus californianus*) haul out on small rocky islands <0.25 km offshore (Lyman 1991). The rocks provide roosting and nesting sites for thousands of sea birds of several species (Murray and Marrant 1983). The beach, rocky shore, rocky islands, estuary, dune, salt marsh, and upland grassland are within minutes by foot or canoe travel of major village sites.

The Salmon River estuary is the smallest of seven major estuaries and bays used by the Tillamook tribe; others are 1.6-12 times its size (Thompson and Snow 1974). The Salmon River estuary has the lowest proportion of submerged and tideland of any of them, and a limited invertebrate fauna. It supports 4 of 16 estuarine invertebrates listed by Thompson and Snow (1974) and Emmett et al. (1991), compared to 5 for the Siletz, 7 for the Nehalem, 11 for Tillamook Bay, and 16 for Netarts Bay. Sand Lake and the Nestucca estuary support fewer of these species than the Salmon River, although they are larger. The estuarine fish fauna is relatively richer (Cornwell et al. 2001). Of 22 major fish species (Emmett et al. 1991), the Salmon River estuary supports 14, compared to 15 in the Siletz estuary, 18 in Netarts Bay, 19 in the Nehalem estuary, and all 22 in Tillamook Bay. Pre-hatchery runs of salmon and steelhead in the Salmon River totaled 4000-5000 fish (Oregon Department of Fish and Wildlife 1997). In 1923-1927, before a major decline, commercial catch of salmon and steelhead from the Salmon River was much less than that in larger systems, 1% that in Tillamook Bay, 2% of the Nehalem, and 4% of the Nestucca and Siletz estuaries (Cleaver 1951).

Extensive red alder (*Alnus rubra*) and conifer forests dominate slopes above the Salmon River valley. The conifers are primarily Sitka spruce (*Picea sitchensis*) near the shoreline, with western hemlock (*Tsuga heterophylla*) becoming important a short distance inland. Several kilometers farther inland, Douglas-fir (*Pseudotsuga menziesii*) becomes abundant and often dominant, and abundance of spruce declines. This forest pattern is not an artifact of logging; it existed in the uncut forests near the time of Euro-American settlement, according to timber cruise records for Tillamook County (Anonymous 1908). Most of the forested area burned in the 1840s (Munger 1944), although areas of old-growth and isolated old trees survived (Greene 1982). The conifer forests are productive and dense, especially when young (Harcombe et al. 1990).

Village sites near the mouth of the Salmon River have been dated to as early as A.D. 1020 (Ross 1990). In 1854, Tillamook people, the southernmost Salish-language group, occupied the area (Beckham et al. 1982). Other Salish-speaking groups lived north of the Columbia River. The Salmon River people, referred to as the Nechesne (also an early name for the Salmon River), Kowai, or Salmon River Indians, continued to live there well into historic time (Beckham 1975, Beckham et al. 1982). Their population was about 10 in 1854 (Beckham et al. 1982), but had probably been reduced by disease before 1840, as had other coastal groups (Seaburg and Miller 1990). The Salmon River people lived primarily by fishing and gathering shellfish, although hunting and use of marshlands and forest were also critical to their survival (Murray and Marrant 1983), like other Oregon coastal groups (Lyman 1991, Connolly 1992, Erlandson et al. 1998). They apparently did not hunt in the open ocean.

The Cascade Head landscape was included in the Siletz Indian Reservation, established in 1855, although the life of the local people probably remained unchanged. Most of the landscape was excluded from the reduced reservation in 1875, although the Salmon River itself remained in the

reservation until 1894 (Beckham 1975). The area appears to have been used as pasture by settlers from the Willamette Valley by 1851. Although early squatters of European lineage settled the north bank of the Salmon River in the 1870s, most settlement occurred in the 1890s, primarily along the lowlands near the Salmon River and Neskowin Creek.

Methods

The primary record about the Salmon River people came from informants for two anthropological studies (Boas 1923, Barnett 1937). Local archeological studies are described by Murray and Marrant (1983) and Beckham et al. (1982). I developed a list of plant and animal species collected, and of their probable uses, by the Salmon River people. I based the list primarily on Barnett's detailed questionnaire (1937), and summaries of local history by Beckham (1975) and Beckham et al. (1982). Secondary sources were Boas' (1923) interview, Murray and Marrant's (1983) excavation, Seaburg and Miller's (1990) tribal summary, and information about other Tillamook villages: Newman's (1959) excavations at Netarts Bay, Sauter and Johnson's (1974) book about people in the Tillamook Bay region, and Zontek's (1978) excavations at Oceanside. Because data about use of plants by the Tillamook were limited, I also included plants for which Salish-speaking groups in southwestern Washington had a distinct name and use (Gunther 1973). Information from Salish language groups in northern Washington and Canada was not used, as they lived in a region culturally different from the Oregon coast (Erlandson et al. 1998).

Species mentioned in works from outside the Cascade Head landscape were counted only if I could confirm their presence in the landscape, either from observation or species lists. In some cases, the exact species identity is uncertain (e.g., several species of bird eggs), but a reasonable estimate of the number could be made. Scientific nomenclature (Tables 1, 2) follows Hitchcock and Cronquist (1973) for plants, Verts and Carraway (1998) for most mammals, Csuti et al. (1997) for birds and amphibians, Maser et al. (1981) for mammals not included in Verts and Carraway, Emmett et al. (1991) for fish and most invertebrates, and Hafele and Hinton (1996) for other invertebrates. I counted uses as in the following example: eating elk meat is one use of elk; wearing elk skins is a second use; fashioning a wood-splitting wedge from elk antler is a third use.

Each species of use was assigned to its most likely origin. For most species, the origin was the type of local ecosystem from which it was easiest to collect, based on ecosystem accessibility to the village sites and species' importance in the ecosystems. Other possible origins were cultivation and trade. Some important fiber plants from freshwater marshes were grouped with salt marsh; they grow on the upper fringes of salt marsh vegetation (Frenkel and Morlan 1990). Elk (*Cervus elaphus*), deer (*Odocoileus hemionis*), bear (*Ursus americanus*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and raccoon (*Procyon lotor*) occur in many habitats, and thus were assigned to a separate category. Similarity of distribution among origins of species and uses (Table 3) was tested using Spearman's rank correlation and the Kolgomorov-Smirnov test.

Other Oregon coastal peoples used many species that occur at Cascade Head but were not counted here (Lindsay 1995), as they were not referred to in literature about the Tillamook. Many useful species undoubtedly went unrecorded, especially those limited to medicinal, ceremonial, or emergency use.

For six widely-used plant species absent or rare in the Cascade Head landscape, I checked distributions of herbarium specimens (ORE, OSC, WILLU) and used the preliminary version of the Oregon Plant Atlas data base (Scott Sundberg, Oregon State University, personal communication) to locate sightings of species.

Results

At least 68 plant and 56 animal species were used by the Salmon River people (Tables 1, 2), with 308 recorded uses, counting multiple uses of a single type (e.g., use of spruce roots in several kinds of baskets). Fifty-two of the 308 uses were associated with a resource, such as wood or bone, without identification of a specific organism, and thus could not be assigned to an origin. To gather the species associated with the 256 uses of an identifiable species, the people used all the major ecosystems in their landscape (Table 3). The most species and uses came from the forests, estuary, and ocean, and many uses from animals that occupy several ecosystems. A few resources

TABLE 1. List of plant species reportedly used by Tillamook people and present in the Cascade Head landscape, with types of use and most likely ecosystem or other origin from which it was obtained.

Type	Common name	Species	Uses[1]	Origin[2]
Fern	Maidenhair fern	*Adiantum pedatum*	BF	A
	Lady-fern	*Athyrium filix-femina*	F	A
	Deer-fern	*Blechnum spicant*	M	S
	Horsetail	*Equisetum* spp.	FI	A
	Licorice-fern	*Polypodium glycyrrhiza*	IM	A
	Sword-fern	*Polystichum munitum*	BFHM	S
	Bracken	*Pteridium aquilinum*	F	G
Tree	Red alder	*Alnus rubra*	BIW	A
	Big-leaf maple	*Acer macrophyllum*	BCI	A
	Sitka spruce	*Picea sitchensis*	BISW	S
	Shore pine	*Pinus contorta*	FIR	D
	Douglas-fir	*Pseudotsuga menziesii*	BW	S
	Cascara	*Rhamnus purshiana*	M	A
	Western yew	*Taxus brevifolia*	IRS	S[3]
	Western redcedar	*Thuja plicata*	BHIS	S
	Western hemlock	*Tsuga heterophylla*	BIW	S
Shrub	Vine maple	*Acer circinatum*	BIS	A
	Serviceberry	*Amelanchier alnifolia*	F	G
	Kinnikinnick	*Arctostaphylos uva-ursi*	FRS	D
	Hairy manzanita	*A. columbiana*	F	D[3]
	Hazelnut	*Corylus cornuta*	BI	S[3]
	Salal	*Gaultheria shallon*	FM	S
	Oceanspray	*Holodiscus discolor*	IM	D
	Twin-berry	*Lonicera involucrata*	FM	D
	Currant	*Ribes* spp. *(3)*	F	S,A
	Rose	*Rosa nutkana*	F	A
	Thimbleberry	*Rubus parviflorus*	BF	S
	Salmonberry	*R. spectabilis*	F	A
	Willow	*Salix hookeriana*	CIS	D
	Red elderberry	*Sambucus racemosa*	FM	A
	Evergreen huckleberry	*Vaccinium ovatum*	F	D
	Huckleberry	*V. ovalifolium*	F	S
	Red huckleberry	*V. parvifolium*	FR	A
Forb	Yellow sandverbena	*Abronia latifolia*	F	D
	Yarrow	*Achillea millefolium*	MR	G
	Wild onion	*Allium* sp.	F	G
	Angelica	*Angelica hendersonii*	FS	M
	Camas	*Camassia quamash*	F	G[3]
	Coast strawberry	*Fragaria chiloensis*	F	D
	Cow parsnip	*Heracleum lanatum*	FM	G
	Waterleaf	*Hydrophyllum tenuipes*	F	A
	Seashore lupine	*Lupinus littoralis*	F	D
	False lily-of-the-valley	*Maianthemum dilitatum*	F	S
	Water-parsley	*Oenanthe sarmentosa*	F	M
	Oregon oxalis	*Oxalis oregana*	FM	S
	Wild tobacco	*Nicotiana quadrivalvis*	RS	C
	Pacific silverweed	*Potentilla pacifica*	F	M
	Wapato	*Sagittaria latifolia*	F	T
	Goldenrod	*Solidago spathulata*	F	D[3]
	Stinging nettle	*Urtica dioica*	FS	A
	Edible thistle	*Cirsium edule*	F	G
Grass-like	Bentgrass	*Agrostis* sp.	F	D
	Brome	*Bromus carinatus*	F	G

Continued, next page

TABLE 1. Continued.

Type	Common name	Species	Uses[1]	Origin[2]
	Slough sedge	*Carex obnupta*	F	M
	Red fescue	*Festuca rubra*	F	D
	Baltic rush	*Juncus balticus*	H	M
	Salt rush	*J. lesueurii*	H	M
	Coastline bluegrass	*Poa confinis*	F	D
	Small-fruited bulrush	*Scirpus microcarpus*	BCF	M
	Seaside arrow-grass	*Triglochin maritimum*	F	M
	Tall trisetum	*Trisetum canescens*	F	G
	Beargrass	*Xerophyllum tenax*	BC	S[3]
	"Reeds"	-	BCH	M
Algae	"Kelp"	-	I	O
	"Seaweeds"	-	FI	E
Moss	"Moss"	-	H	S

[1]Types of usage: B = containers, such as baskets, boxes, or liners for them; C = clothing; F = food; H = housing or bedding, including mats; I = implements, including canoe, bow, wiper, needle, rope, fish club...; M = medicinal use; R = recreational use, including ornaments, games, or smoking; S = ceremonial use by the shaman or in dances or other ceremonies; W = firewood. Other uses of plants not identified to species: wood, 28; grass, 3; fiber, 2; rotten wood, 1.
[2]Origin: T = probably by trade; C = cultivated; other letters indicate the ecosystem from which the species was most likely to be collected—A = alder forest, D = dune grassland or dune forest, E = estuary, G = headland grassland, M = marsh, both salt marsh and bordering freshwater marsh, O = ocean and its shores, S = spruce-hemlock forest.
[3]indicates that the species is not listed for the landscape, but may have been collected elsewhere within territory controlled by the group.

TABLE 2. List of animal species noted in lists of uses by Tillamook people, with types of use and most likely ecosystems or other origins from which they were obtained.

Type	Common name	Scientific name	Uses[1,2]	Origin[3]
Mollusc	Chiton	—	F	O
	Clam	*Tresus nuttalli*	BFI$	O[4]
	Cockle	*Clinocardium nutallii*	F	O
	Dentalium	*Dentalium pretiosum*	S$	T
	Mussel	*Mytilus* sp.	FI	O
	Octopus	*Octopus dofleini*	F	O
	Olivella shell	*Oliviella biplicata*	S	O
	Red abalone	*Haliotis rufescens*	S	T
	River clam	—	F	E
	Snail	—	F	O
Crustacean	Barnacle	—	F	O
	Crab	*Cancer magister*	F	E
	Crawfish	*Pacifastacus* sp.	I	A
Fish	Chinook salmon	*Oncorhynchus tshawytscha*	FI	E
	Chum salmon	*Oncorhynchus keta*	FI	E
	Coho salmon	*Oncorhynchus kisutch*	FI	E
	Herring or smelt	—	F	E
	Lamprey	*Entosphenus tridentatus*	F	E
	"Mudcat"	—	I	E
	Starry flounder	*Platichthys stellatus*	F	E
Amphibian	Rough-skin newt	*Taricha granulosa*	S	A
Bird	Duck (5 spp.)	—	FI	E
	Eagle	*Haliaeetus leucocephalus*	S	S
	Goose	*Branta canadensis*	FI	E
	Hummingbird	—	S	A

Continued, next page

TABLE 2. Continued.

Type	Common name	Scientific name	Uses[1,2]	Origin[3]
	Seagull (>1 spp.) eggs	—	F	O
	Woodpecker	—	S$	A
	Unspecified sea bird (>1 spp.) eggs and young	—	F	O
Mammal, marine	California sea lion	*Zalophus californianus*	BCF	O
	Harbor seal	*Phoca vitulina*	BCF	O
	Porpoise	*Phocoena phocoena*	F	O
	Sea otter	*Enhydra lutris*	CH	O
	Steller's sea lion	*Eumetopias jubatus*	BCF	O
	Gray whale	*Eschrichtius robustus*	BFI	O
Mammal, terrestrial	Black bear	*Ursus americanus*	CFS	W
	Beaver	*Castor canadensis*	FHIR	A
	Chipmunk	*Tamias townsendii*	CF	S
	Deer	*Odocoileus hemionus*	BCFHIS	W
	Dog	*Canis familiaris*	FR	C
	Elk	*Cervus elaphus*	BCFHIM	W
	Mink	*Mustela vison*	RS	M
	Mole	*Scapanus* sp.	B	G
	Mountain lion	*Puma concolor*	C	W
	Rabbits	*Sylvilagus bachmani, Lepus americanus*	FCIR	S
	Raccoon	*Procyon lotor*	CF	W
	River otter	*Lutra canadensis*	CS	E
	"Sheep" (mountain goat)	*Oreamnos americanus*	H	T
	Douglas' squirrel	*Tamiasciurus douglasii*	CF	S
	Long-tailed weasel	*Mustela frenata*	B	S
	Wildcat (bobcat)	*Lynx rufus*	C	W

[1]Types of usage: B = containers such as bags, or liners for containers; C = clothing; F = food; H = housing or bedding; I = implements, including canoe, bow, wiper, needle, rope, fish club...; M = medicinal use; R = recreational use, including ornaments, games, or smoking; S = ceremonial use by the shaman or in dances or other ceremonies; $ = currency.
[2]Uses of animals not identified as to species: bird bone, I, R; bone, IS; skin, BHI; antler, CI; feathers, IS.
[3]Origin: C = domesticated animal, T = probably by trade; other letters indicate the ecosystem from which the species was most likely to be collected—A = alder forest, D = dune grassland or dune forest, E = estuary, G = grassland, M = marsh, both salt marsh and bordering freshwater marsh, O = ocean and its shores, S = spruce-hemlock forest, W = moved widely through several ecosystems.
[4] indicates that the species is not listed for the landscape, but may have been collected elsewhere within territory controlled by the group.

must have come from trade. The Tillamook cultivated tobacco, as did other western Oregon tribes, apparently their only attempt at farming. Domesticated dog bones occur in Salmon River middens; food seems their most likely use (Murray and Marrant 1983).

The proportions of species and uses (Table 3) among ecosystems were significantly correlated (Spearman's rank correlation coefficient r = 0.81, $p = 0.015$); i.e., there were more uses where there were more species. The distribution of uses among origins did not differ from that of species (K-S statistic = 0.447); i.e., there was not a significant concentration of highly used species in a few ecosystems.

There were many documented uses for large mammals and some trees, including elk, deer, sea lion, whale, western redcedar (*Thuja plicata*), and

TABLE 3. Percentages of species and recorded or probable uses of biological materials for the indigenous peoples in the Cascade Head landscape, by their most likely ecosystem of origin or other origin. Percentages are for 124 species and 256 uses attributable to an origin. See text for basis of assignment to ecosystems.

Ecosystem or other origin	Percentage of species	Percentage of uses
Ocean	11	11
Estuary	14	11
Dune/beach	10	10
Salt marsh	10	7
Alder forest	15	17
Conifer forest	20	24
Headland grassland	8	6
Roam through several	6	14
Cultivated	2	1
Acquired by trade	5	4

red alder. Uses were best documented for antler, shell, and bone implements. Multiple uses of wood, many recorded or inferred to be western redcedar, are indicated by Barnett's (1937) informant and for other Tillamook areas (Newman 1959, Sauter and Johnson 1974, Beckham et al. 1982).

Some important plant resources for coastal tribes were rare or absent from the Cascade Head landscape. Western redcedar was not recorded in the Tillamook County portion of the landscape in 1908 (Anonymous 1908). In the 1934 timber cruise of the Cascade Head Experimental Forest, this species made up only 0.26% of timber volume (USDA Forest Service 1938) and was recorded no closer than 2.6 km to the estuary. It grew 9 km south, also, probably within territory of the villages. Yew (*Taxus brevifolia*), preferred for bows and arrows by the Salmon River people (Barnett 1937), is absent from the study area. Although yew grows in many Coast Range forest types, including two with Sitka spruce (Hemstrom and Logan 1986), the nearest record is from 92 km NNE. Hazel (*Corylus cornuta*), a major material for baskets and rope, is widespread in inland Coast Range forests, but almost absent where spruce dominates (Hemstrom and Logan 1986); it has been collected on the coast at Sand Lake, 25 km N of the Salmon River and near the coast 36 km S. Camas (*Camassia* spp.), widely reported as a staple food plant, has not been collected in the Cascade Head landscape, but herbarium specimens show that it grew at Devil's Lake, at least 4 km S and probably within the territory of the Salmon River villages. Otherwise, camas is rare on the central and north-central coast, but does occur in meadows near and east of the crest of the Coast Range. The current herbaceous vegetation in the Salmon River valley, where one might expect camas to have grown, was probably riparian forest before it was converted to pasture (USDA Forest Service 1999). Big-leaf maple (*Acer macrophyllum*), an important source of fiber and wood, is uncommon in the landscape, in forests with spruce (Hemstrom and Logan 1986), and in this region in general (Hines 1971). Maple grows abundantly in the Coast Range, probably within territory controlled by the Salmon River people. Beargrass (*Xerophyllum tenax*) is absent from the landscape, but is reported from forest types that grow on the eastern fringe of the watershed. The nearest specific record is from 92 km NNE.

Some commonly used animals also are apparently absent from the landscape. The soft-shelled clam (*Mya arenaria*), probably introduced, is the only clam reported from the Salmon River (Thompson and Snow 1974), although shell from gaper clam (*Tresus* sp.) is present in local shell middens (Beckham et al. 1982). Of seven invertebrates found in middens farther north in Tillamook territory (Barner 1982), only three grow or were found in middens at the Salmon River (Beckham et al. 1982). Mussels (*Mytilus* sp.) were the most commonly used invertebrates (Murray and Marrant 1983), as elsewhere on the Oregon coast (Lindsay 1995). More fish than named in Table 2 were probably used: Oregon coastal peoples appear to have eaten most that were available and collected them year-round (Erlandson et al. 1998), and 24 species have been identified from middens at Seaside (Connolly 1992), on the northern fringe of Tillamook occupancy during the historic period.

Discussion

Data from studies of ethnography, archeology, and distribution of organisms share some problems of interpretation. Sampling is sparse compared to the time and territory it is usually used to represent. Absence of an item from the record cannot assure its absence from indigenous use or the landscape. In this study, most data about plant usage are recent, from interviews of tribal members who survived until at least 1890 (Boas 1923). Many data about animal use, in contrast, came from excavation of earlier middens deposits, AD 900-1675 (Newman 1959, Ross 1990, Erlandson and Moss 1995). Data for organism distribution date from 1908 to (usually) after 1970.

Two major changes in vegetation occurred near the time of contact with Europeans. About AD 1700, subsidence during an earthquake and burial by a tsunami deposit modified estuarine habitats (Minor and Grant 1996); marsh vegetation in the estuary probably recovered within several decades. In the 1840s, a large, intense fire killed most forest in the landscape (Munger 1944). Informants for ethnographic studies grew up amidst young forest that developed after fire. Their statements to anthropologists may have differed from those appropriate for preceding generations. Old-growth forest that survived the fire is of similar composition to forest that developed after the fire (Greene

1982); thus, it seems unlikely that the 1840s fire caused the local scarcity of western redcedar. Effects of management with fire, used by the Tillamook to make berries, game animals, and perhaps camas more available (Sauter and Johnson 1974, Boyd 1999), would have disappeared. Although the comparisons of resource usage and availability in this study seem reasonable, many data for usage of resources, and all data for organism distribution and abundance, may include changes after the time of European contact.

Except for materials that survived burial, data about usage depend on the sparse records of early Euro-American explorers and residents, and experience and memory of a few informants. Usefulness of many species may not have been recorded for the Tillamook. For example, 17 grassland plant species present at Cascade Head but absent from Table 1 were used or possibly used by the indigenous peoples of the prairies of western Washington (Norton 1979), and an additional six were famine foods of northwestern coastal tribes (Turner and Davis 1993). Detailed analysis of faunal remains at Seaside, Oregon, just north of Tillamook territory, identified at least 24 fish taxa and 30 bird taxa (Connolly 1992), many more than listed in Table 2.

Obtaining appropriate distribution data for this type of study is also difficult. Published range maps (Little 1971, Csuti et al. 1997) show general aspects of organism distribution, but abundance and even presence vary within the ranges shown on maps. Data from detailed vegetation survey plots and specimen collections illustrate the maps' failure to display the details of distribution required for a study of this type (Anonymous 1908, Hemstrom and Logan 1986, Emmett et al. 1991).

Table 3 probably underestimates the importance of some of the lesser-used ecosystems. For example, grasslands are represented in Tables 1 and 2 only by food plants and moles, but were managed by Tillamook people to improve hunting of elk and deer (Sauter and Johnson 1974), which are assigned to no specific ecosystem and could be captured in a variety of ways in several ecosystems (Barnett 1937). The Salmon River people had easy access to a large grassland where elk and deer graze, which has cliffs along much of its perimeter. Elk bones were common in middens at the mouth of the river (Beckham et al. 1982, Murray and Marrant 1983).

Not all resources for which use is claimed by or attributed to the Salmon River people grow in the vicinity of known villages. Four important materials probably came from trade: the dentalium (*Dentalium pretiosum*) and red abalone (*Haliotis rufescens*) shells, widely used for currency and decoration throughout the northwest coast; mountain goat (*Oreamnos americanus*) hair for blankets; and wapato tubers (*Saggitaria latifolia*) for food. Wapato may have been traded from east of the Coast Range (Beckham et al. 1982), because access through the mountains was relatively easy. Woven blankets in coastal Oregon probably came from imported mountain goat wool, rather than mountain sheep; in contrast, coast Salish farther north used hair of domesticated dogs (Howay 1918). In addition, it is unclear whether beargrass leaves, used to decorate woven items, and camas, as food, were available to the Salmon River people. Where camas was absent, people traded for it (Gunther 1973).

Some resources absent from the landscape may have been available in the inland territory controlled by the village, which extended to the crest of the Coast Range (Beckham et al. 1982), including beargrass (Hines 1971), camas, yew, and hazel. These resources are easily transported. There is evidence that residence at the Salmon River estuary was seasonal, during fall and winter (Murray and Marrant 1983), presumably with residence farther inland in other seasons. Big-leaf maple is present at Cascade Head in small numbers, but abundant inland within territory controlled by the village.

The most important scarcity in the Cascade Head landscape was western redcedar. Availability of large western redcedar trees revolutionized the culture of coastal peoples in British Columbia as cedar migrated into their territory during post-glacial warming (Hebda and Mathewes 1984). Local spatial variation in its importance on the Oregon coast seems likely to have affected culture, also. According to Barnett's (1937) informant, a Salmon River native, houses had matlined dirt walls, and walls and roof were not made of planks or bark. Wood (type unspecified) was used for beams, posts, and the sweathouse roof. House construction without cedar planks differs from the standard Tillamook and coastal practice. Beckham (1975) cites Barnett (1937) but also states that Salmon River people built plank houses. Newman (1959) explicitly dismisses Barnett's

informant's statement, citing the planked houses he had excavated at Netarts Bay and Boas (1923) as his reasons. On the other hand, one of Newman's houses apparently had not been of planks, and Boas (1923) noted that poor people sometimes lived in grass houses both in winter and summer. It seems likely that building houses without cedar was necessary, due to its scarcity near the Salmon River villages. Cedar was used for canoes (Barnett 1937), the usual regional custom. Canoes were an important item of trade (Seaburg and Miller 1990), whereas moving house planks many meters long (Newman 1959) for kilometer distances may not have been feasible.

The scarcity of several plants considered standard resources for Oregon coastal peoples, especially cedar and camas, may have limited the population and wealth of the Salmon River people. In addition, they lived near a small, primarily marshy estuary (with limited invertebrate diversity) of a small river (with relatively small fish runs). Access to extensive rocky coastline required ocean travel, not feasible during stormy weather. There are no estimates of population before the introduction of disease that accompanied contact with European traders. These villages, although located optimally amidst river, estuary, sandy and rocky shore, ocean (Erlandson et al. 1998), upland grassland, and forest, appear to have less potential for wealth than situations usually described for Tillamook and other coastal Oregon tribes. Previously unrecognized differences in resource availability may have caused unrecognized variation in size, wealth, and trade of different villages.

In conclusion, all local ecosystems were important sources of organisms for Salmon River people. Even so, the Cascade Head region could not supply all important species used by the Tillamook tribe. Trade supplied some needs. Collecting throughout their extensive territory away from coastal villages probably supplied others. In the case of cedar for houses, however, the people apparently had to do without.

Acknowledgements

This research was supported by a residency at the Sitka Center for Art and Ecology, Otis, Oregon, provided by the Neskowin Coast Foundation, and by sabbatical support from Oregon State University. I appreciate the comments on a draft of this paper by Roberta Hall, Sarah Greene, Kenneth Ames, Jon Erlandson, and Mark Merlin. Thanks to Richard Halse and Scott Sundberg for help determining plant distributions.

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Received 5 December 2001
Accepted for publication 16 May 2002

David M. Braun, Bi Runcheng, David C. Shaw,[1] and **Mark VanScoy,** University of Washington, Wind River Canopy Crane Research Facility, 1262 Hemlock Rd., Carson, Washington 98610

Folivory of Vine Maple in an Old-growth Douglas-fir-Western Hemlock Forest

Abstract

Folivory of vine maple was documented in an old-growth Douglas-fir-western hemlock forest in southwest Washington. Leaf consumption by lepidopteran larvae was estimated with a sample of 450 tagged leaves visited weekly from 7 May to 11 October, the period from bud break to leaf drop. Lepidopteran taxa were identified by handpicking larvae from additional shrubs and rearing to adult. Weekly folivory peaked in May at 1.2%, after which it was 0.2% to 0.7% through mid October. Cumulative seasonal herbivory was 9.9% of leaf area. The lepidopteran folivore guild consisted of at least 22 taxa. Nearly all individuals were represented by eight taxa in the Geometridae, Tortricidae, and Gelechiidae. Few herbivores from other insect orders were observed, suggesting that the folivore guild of vine maple is dominated by these polyphagous lepidopterans. Vine maple folivory was a significant component of stand folivory, comparable to ~ 66% of the folivory of the three main overstory conifers. Because vine maple is a regionally widespread, often dominant understory shrub, it may be a significant influence on forest lepidopteran communities and leaf-based food webs.

Introduction

Herbivory in forested ecosystems consists of the consumption of foliage, phloem, sap, and live woody tissue by animals. Typical insect-produced herbivory levels of 7.1% for temperate forests and 11.1% for shade-tolerant species in the humid tropics have been reported, based on leaf area loss (Coley and Barone 1996). In contrast, occasional folivore outbreaks of the western spruce budworm (*Choristoneura occidentalis*) (Tortricidae) (Brookes, 1987) or the western hemlock looper (*Lambdina fiscellaria lugubrosa*) (Geometridae) (Harris et al. 1982) in temperate conifer forest can produce defoliation approaching 100%. Herbivory also varies spatially, for example, from 1% to 54% along an elevation gradient in Australia (Lowman 1995). Studies are usually restricted to measuring holes produced by leaf chewing arthropods, and therefore describe folivory alone.

Old-growth conifer forests in the Pacific Northwest west of the Cascade Range crest tend not to have defoliator outbreaks (Perry and Pitman 1983). Exceptions are outbreaks of geometrids, such as the western hemlock looper. This moth occasionally produces patches of intense defoliation in old-growth stands dominated by western hemlock (*Tsuga heterophylla*) (Harris et al. 1982). In contrast to defoliator outbreaks, less is known about endemic populations of defoliators and low-level folivory.

Vine maple (*Acer circinatum*) is one of the dominant shrubs in forest communities in the zone of maritime climatic influence in Oregon and Washington from the crest of the Cascade Mountains to the Pacific Ocean (Franklin and Dyrness 1988), and in coastal British Columbia (Haeussler et al. 1990). The shrub typically grows in clumps that enlarge vegetatively through resprouting and layering, and persists through multiple disturbances and successional stages (Schoonmaker and McKee 1988, Haeussler et al. 1990, Tappeiner and Zasada 1993, O'Dea et al. 1995). Mature vine maples are usually several meters tall with irregularly shaped crowns that have foliage arranged in flattened irregular sprays (Haeussler et al. 1990, O'Dea et al. 1995).

Even though vine maple is a common species in the Pacific Northwest, little information has been published on its herbivory and insect herbivores. Known folivores are generalist feeders (Furniss and Carolin 1980, Miller 1995). One report states that herbivory is low (Taylor 1976). Reported folivores include the tussock moths (*Orgyia*) (Lymantriidae), the polyphemus moth (*Antheraea polyphemus*) (Saturniidae), and the brown day moth (*Hemileuca eglanterina*) (Saturniidae) (Taylor 1976). The western hemlock looper feeds on vine maple during outbreaks on its principle host,

[1]Author to whom correspondence should be addressed. E-mail: dshaw@u.washington.edu

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western hemlock (Furniss and Carolin 1980). Other maples have been better documented; for example, the herbivory of red maple, a common tree in eastern North America, has been reported at 2% to 10% (Reynolds and Crossley 1997).

The presence of a generalist folivore guild on vine maple can be predicted based on the common shrub's perennial growth form, likely chemical defenses against herbivory and common occurrence within its range. Long-lived, common plants typically have tannins, digestibility reducing phenolic compounds, as the main anti-herbivory chemicals (Feeny 1980, Rhoades and Cates 1976). Condensed tannins and lignins become more concentrated as leaves age, decreasing leaf palatability and digestibility, whereas labile hydrolysable tannins increase in response to herbivory (Rhoades 1979). Although the defensive chemistry of vine maple has not been reported, it is probably similar to several other maples for which a tannin and lignin based defense has been described (Bate-Smith 1977, Seastedt et al. 1983, Hunter and Lechowicz 1992, Shure and Wilson 1993, Shure et al. 1998). As maple leaves mature and age, greater lignin content increases leaf toughness, inhibiting folivory. Lepidopteran larvae may exhibit a spring feeding strategy to avoid these defenses (Hagen and Chabat 1985, Shure and Wilson 1993).

The purpose of this study was to quantify vine maple herbivory and describe the folivore guild. We described temporal and spatial folivory patterns in addition to producing an overall folivory estimate.

Methods

Study Site

Three study sites were selected in a 500 year-old Douglas-fir-western hemlock forest in the southern Washington Cascades, in and adjacent to the T. T. Munger Research Natural Area (the RNA), Gifford Pinchot National Forest. The RNA was established in 1934 for the study of forest dominated by Douglas-fir (*Pseudotsuga menziesii*), and it is the location of a stationary canopy access crane erected in 1995. One site was near the crane, and all were within 1.2 km of each other in the same stand.

The environment of the RNA reflects its submontane location just west of the crest of the Cascade Range, at an elevation of 360-380 m in the Trout Creek drainage (Franklin 1972, Shaw et al. 2001). Precipitation is 247 cm per year, occurring partly as snow, and average minimum and maximum temperatures are 0.5°C and 12.3°C. Soils underlying the sites are well drained because of volcanic tephra parent material, and are moderately fertile.

The stand is typical in structure for an old-growth conifer forest in the western hemlock zone dominated by Douglas-fir, western hemlock, and western red cedar (*Thuja plicata*) (Franklin 1972, Franklin and Dyrness 1988, Franklin and DeBell 1988, Parker 1997). The study sites were located in relatively dry western hemlock associations (Topik et al. 1986), described as the western hemlock/Oregon grape-salal, western hemlock/salal complex (Meyers and Fredricks 1993). Vine maple was widespread at each site, and had been estimated at 26.7% cover near one site (Shaw et al. 2001).

Herbivory in the RNA is low. Bark beetles have probably produced the largest herbivore impact, by periodically killing mature Douglas-fir and western white pine (*Pinus monticola*) (Franklin and DeBell 1988). Western hemlock looper outbreaks have not been observed in the RNA from the time it was established in 1934 (Franklin and DeBell 1988). Folivory estimates of 3% or less have been made for the three dominant conifer species in the 2.3 ha area accessed by the crane (Shaw and Baker 1996, Schowalter and Ganio 1998). Limited defoliation by the silver spotted tiger moth (*Lophocampa argentata*) has been observed in the upper crowns of Douglas-fir and western hemlock in this area (Shaw 1998).

Folivory

Folivory was estimated by repeated observations of 450 leaves to track intra-seasonal folivory. At each of the three sites, 10 leaves were tagged on each of 5 shrubs arrayed on 3 transects. Leaves were tagged on the petiole with a loop of dental floss and a small piece of flagging, and were observed 23 times from 7 May to 9 October 1999. Both shrubs and transects were approximately 50 m apart. Some shrubs were excluded that had less than 200 leaves.

Leaves were selected by dividing each crown into 10 equal sectors originating at a central point, and selecting the outer-most leaf in each. This

approach was utilized to sample the irregular, planar, 3-5 m tall crowns systematically while seeking to avoid disturbance of resident arthropods. Because foliage was in flattened arrays along branches that were at multiple heights and had little vertical overlap, selected leaves were in a wide range of distances from shrub centers and the ground. However, leaves towards the centers of foliage planes may have been under-represented. Selected leaves varied in height from 8 to 430 cm, with a mean of 160.8 ± 2.8 cm., and varied in area from 11 to 96 cm^2, with a mean of 38 ± 0.7 cm^2.

Folivory estimates were based on percentage leaf area lost calculated for individual leaves, a method reported by Lowman (1984). Periodic and seasonal folivory estimates were means of leaf percentages. To estimate folivory on each leaf, the area consumed was visually measured with a clear plastic grid to an accuracy of 0.1 cm. Folivory was defined as the loss of leaf area for attached leaves. If an entire leaf and petiole were absent, no herbivory was recorded on the observation date. Sketches were made of leaf outlines and holes to aid in distinguishing new feeding. Holes were defined as the new areas consumed from one week to the next.

Folivore Guild

Sampling was limited to lepidopterans because populations of other orders were extremely low. Occasional aphids and leafhoppers (Homoptera: Aphididae and Cicadellidae) were observed, but leaf beetles were not (Coleoptera: Chrysomelidae).

Larvae were collected on separate transects 10 - 20 m away from each folivory transect. On each visit, a target number of five larvae were hand-picked from a new shrub on each transect. Ten collections were made between 1200 and 1700 hr from 18 May to 18 August.

Larvae were reared with vine maple leaves as food. At the end of the season, remaining pupae were refrigerated for one month at 4.5°C to complete the development of fall-emerging species. Species identifications based on larval anatomy were made with reference to Miller (1995); species identifications of larvae and pinned adults were confirmed by Jeffrey Miller and Paul Hammond, Department of Entomology, Oregon State University.

Statistical and Graphical Analysis

The similarity of the three sites was examined to justify pooling leaf consumption data for an overall folivory estimate. The arcsine transformation was applied to individual leaf percentages to normalize the data before statistical analysis (Seastedt et al. 1983, Zar 1999). Analysis of variance was performed to compare the percentage folivory among sites, with sites as the single random factor. Correlation among folivory and spatial variables (total leaf folivory, number of holes per leaf, leaf height, and size) was explored with the Spearman Rank test (Zar 1999).

Graphical analysis was used to assess sampling rigor. The mean and standard error of increasingly large subsets of leaf folivory were plotted over subset size, and repeated for multiple random orderings of the leaf folivory data. A range for the mean and standard error of a sample size less than the total could then be estimated.

Results

Folivory

Folivory was estimated within the entire foliated period for vine maple, based on phenological observations (Braun, 2002). Bud break occurred within several days of 1 May, and leaf expansion continued for almost 3 wk. Observations were ended on 11 October because many leaves were turning color, signaling the beginning of seasonal leaf drop.

Weekly folivory varied from 0.2 % - 0.8 % on 17 of 23 observation visits. It was below this range at the beginning and end of the seasonal observation period, and peaked in May at 1.2 ± 0.2 % (Figure 1).

The number of leaves observed did not remain constant over the 23 visits from 6 May to 11 October: of the original 450 leaves, 382 leaves (84.9%) remained on the last visit. The initial number of leaves was 438, because 12 leaves abscised before full expansion, precluding folivory estimation based on the area of fully expanded leaves.

Seasonal folivory was the product of up to 26 holes per leaf, with a mean frequency of 4.6 ± 0.2. Holes were most often on leaf edges (50.3%), followed by interior areas (43.3%), and areas adjacent to previous holes (6.2%). The amount of folivory was significantly correlated with holes

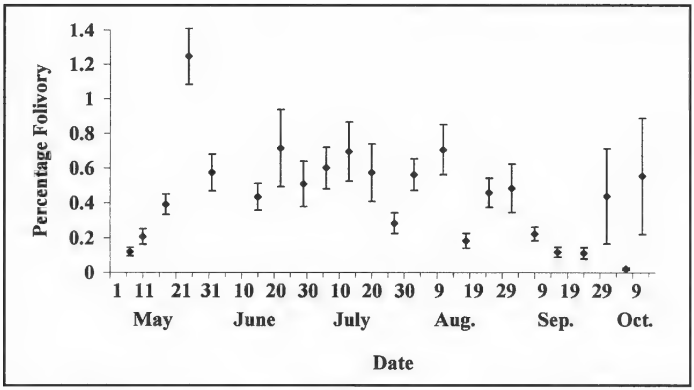

Figure 1. Weekly folivory produced by lepidopteran larvae from 7 May to 11 October 1999 feeding on tagged vine maple leaves. Data are the mean percentages of missing portions divided by fully expanded leaf area.

per leaf, but not with leaf size or leaf height. There was no significant correlation among holes per leaf, size, or height.

The validity of pooling folivory data was supported by the results of an analysis of variance comparing folivory among the sites. The sites were not significantly different from each other. Means for individual sites were 8.7% ± 1.0, 10.0% ± 1.2, and 10.9% ± 1.2.

The sufficiency of folivory sampling intensity was supported by the stability of the mean and standard error at less than the total sampling effort. Based on five random orderings of leaf folivory, these statistics became focused in narrow ranges beginning with about half the sample leaves (Figure 2a, b). Based on 50%, 90%, and 100% of leaves, mean folivory was 9.0% - 10.3% (SE 0.8 - 1.1), 9.9% - 10.2% (SE 0.7), and 9.9% (SE 0.7).

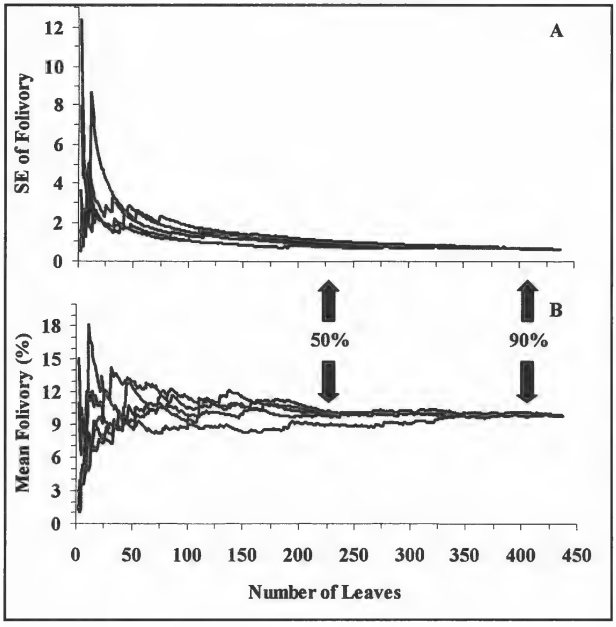

Figure 2. Plots of the mean (A) and the standard error (B) generated by cumulative resamples of the seasonal folivory of 2 to 438 vine maple leaves arranged in five random rankings.

Folivore Guild

Larval collection visits yielded 397 larvae of which 389 were assigned to taxa at the family level or below (Table 1). Thirteen taxa were distinguished at the species level, increasing the number of previously reported species known to feed on vine maple by 11.

Taxonomic identifications were based on reared adults, slides of larvae, and descriptive notes. Because only about 10% of the eight common taxa were successfully reared to adult, these were assigned to major groups based on family membership and temporal occurrence (Table 1). None of the less common taxa, represented by

TABLE 1. Lepidopteran larvae collected from vine maple in an old-growth Douglas-fir-western hemlock forest in 1999[1].

	May			June			July			August
	18	21	28	4	17	24	1	14	28	20
Major Groups:										
Early Geometridae	36	46	37	29	0	0	0	0	0	0
Tortricidae	0	0	0	5	5	0	1	1	0	1
Late Geometridae	0	0	0	0	31	45	28	2	1	0
Gelechiidae	0	0	0	0	0	1	8	38	32	20
Other Geometridae:										
Erannis tiliaria	0	0	0	0	0	2	0	0	0	0
Eupithecia sp.	0	0	0	0	0	0	1	0	0	0
Iridopsis emasculata	0	0	0	0	1	0	0	2	0	0
Per mizon	0	0	0	0	1	0	0	0	0	0
Geometrid 1	0	0	1	0	0	0	0	0	0	0
Geometrid 2	0	0	0	0	0	0	0	1	0	0
Geometrid 3	0	0	0	0	0	0	0	0	1	3
Noctuidae:										
Lithophane georgii	0	0	0	0	0	0	0	0	0	1
Amphipyra pyramidoides	0	1	1	1	0	0	0	0	0	0
Phlogophora periculosa	0	0	0	0	1	0	0	0	0	0
Zale sp.	0	0	0	0	0	0	1	0	0	0
Noctuid 1	0	0	0	3	0	0	0	0	0	0
Lasiocampidae:										
Phyllodesma americana	0	0	0	0	0	0	0	0	1	0
Saturniidae:										
Antheraea polyphemus	0	0	0	0	0	0	0	0	1	0
Total:	36	47	39	38	39	48	39	44	36	25

[1]Taxa of the Major Groups were as follows: early geometrids: *Operophtera bruceata*; tortricids:*Choristoneura rosaceana*, *Archips* sp., and *Acleris* sp.; late geometrids: *Itame plumosata*, *Lambdina fiscellaria lugubrosa*, and *Neoalcis californiaria*; gelechiids: one or more species.

three or fewer individuals, was successfully reared. However, because many taxa have distinctive larval characteristics, 13 of the 22 taxa were identified to species.

Four groups representing at least eight taxa made up the bulk of the collections (Table 1). The first group was present in May and early June and consisted solely of a geometrid, the Bruce spanworm (*Operophtera bruceata*). The second group was present from mid-June to early July and consisted of geometrids: the western hemlock looper, the brown-lined looper (*Neoalcis californiaria*), and *Itame plumosata*. The third group was present from June through August and consisted of at least three tortricids: the obliquebanded leafroller (*Choristoneura rosaceana*), and *Acleris* and *Archips* species. The fourth group, present from early July to late August, consisted of at least one species of a microlepidopteran family, the Gelechiidae.

Low numbers of individuals in at least 14 additional taxa were collected or observed (Table 1). Geometrid taxa consisted of the linden looper (*Erannis tiliaria*), *Eupithecia* sp., *Iridopsis emasculata*, *Pero mizon*, and three unknowns. Noctuid taxa consisted of *Lithophane georgii*, the copper underwing (*Amphipyra pyramidoides*), *Phlogophora periculosa*, *Zale* sp., and one unknown. One lasiocampid, the lappet moth (*Phyllodesma americana*) was collected. One saturniid, the polyphemus moth (*Antheraea polyphemus*) was observed in September on an herbivory transect but not collected; it was identified by its distinctive large size and coloration.

Discussion

The 9.9% folivory is similar to the level reported elsewhere for temperate broadleaved trees, including maples (Seastedt et al. 1983, Reynolds and Crossley 1997). This amount may be a significant

portion of stand folivory. Based on the projected leaf area of vine maple relative to the conifers in the stand, 0.4 m^2 compared to 6.5 m^2 leaf area/m^2 forest floor (Thomas and Winner 2000), vine maple folivory represented ~66% of the amount of conifer leaf area consumed, if conifer folivory of 1% is typical.

All identified species were polyphagous (Brown 1962, Furniss and Carolin 1980, Carriere et al. 1995, Miller 1995), confirming our prediction of a lepidopteran community dominated by generalists. Three of the species also feed on conifers, reflecting wide host ranges; these are the western hemlock looper, the obliquebanded leafroller (Carriere et al. 1995), and *Neoalcis californiaria* (Furniss and Carolin 1980). The Bruce spanworm, the most commonly collected taxon in this study, feeds on a wide range of other broadleaved trees and shrubs: alder, apple, blueberry, cherry, hazel, maple, poplar, rose, serviceberry, and willow (Brown 1962, Troubridge and Fitzpatrick 1993, Carriere et al. 1995, Miller 1995). Because members of these host plant genera are common in the stand and greater Wind River drainage (Franklin and Dyrness 1988, Meyers and Fredricks 1993), the identified lepidopteran taxa may be as well.

The sequential nature of the common members of the community may represent adaptations to changes in food quality related to foliage age and folivore damage. In other maple species, leaf toughness and tannin content increase over time, decreasing food value for insect folivores (Hunter and Lechowicz 1992, Shure et al. 1998). Additional studies on food choice may distinguish the importance of host quality from other potential influences on folivore populations, such as competition with other lepidopteran folivores and the avoidance of predators and parasites.

Even though the observed folivores are polyphagous, host choice may shift with population level. During outbreaks, the hemlock looper feeds on western hemlock, its preferred host, and understory shrubs including vine maple (Furniss and Carolin 1980). We commonly found the hemlock looper on vine maple, even though there has not been a hemlock looper outbreak since at least 1934 in the RNA (Franklin and DeBell 1988), suggesting that vine maple may be a preferred host in endemic periods. This hypothesis could be addressed by monitoring the host choice of this looper in the stand.

Our description of a lepidopteran folivore guild containing 22 taxa is conservative. More intensive sampling and greater rearing success would have produced some additional species identifications. Because populations can be expected to vary from year to year, species we described as common may become less so, while others become more common. Multi-year studies in a range of forest communities and successional stages are justified to better understand the role of this shrub and its lepidopteran folivores in forest ecosystems.

Acknowledgements

This research was supported by the Ecosystem Research Group at the University of Washington and the USDA Forest Service Pacific Northwest Research Station, Portland. Thanks are offered to Jeffrey Miller and Paul Hammond, Oregon State University, for help in species identification, and Melinda Davis, Whitman College, for help in rearing larvae.

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Received 11 June 2001
Accepted for publication 16 April 2002

David C. Shaw[1], **Elizabeth A. Freeman,** and **Catherine Flick,** Wind River Canopy Crane Research Facility, University of Washington, 1262 Hemlock Road, Carson, Washington 98610

The Vertical Occurrence of Small Birds in an Old-growth Douglas-fir-Western Hemlock Forest Stand

Abstract

The vertical occurrence of the small bird assemblage (songbirds, small woodpeckers, nighthawks, and swifts) in a ~4 ha stand within the T.T. Munger Research Natural Area, a 500 yr old Douglas-fir-western hemlock forest, was quantified to characterize this assemblage and determine whether birds are vertically stratified within the canopy. We used a gondola suspended from a construction crane to count birds in a weekly series of vertically stratified fixed-area point counts, 5-min, 30 m radius, in the lower (0-20 m), mid (21-40 m) and upper (41-60+ m) canopy. Data are from 21 March 1996 to 21 March 1999, and included 121 survey days (mean 40 counts/yr, March-June 42, July-October 46, November-February 33). Twenty-nine species of birds were detected in the plots; the 20 most common were used for analysis. Fifteen of these species were detected significantly more often in one zone of the canopy. Timber foliage insectivores, air insectivores, timber seed-eaters, and most low understory herbivore-insectivores were stratified within the canopy. Bark insectivores (except brown creeper) and omnivore-scavengers (except gray jay), however, were not stratified within the canopy. The number of bird detections shifted to the upper canopy during winter. One species was generally restricted to the lower canopy, and five species were restricted to the upper canopy, whereas no species were found exclusively in the mid-canopy. The small bird assemblage of this old-growth forest stand was vertically and seasonally patterned and the vertical forest structure, particularly within the upper canopy, reflects these patterns.

Introduction

Characterization of the vertical pattern of avian occurrence in a plant community is a key aspect of understanding terrestrial bird assemblages. Dunlavy (1935) recognized the term phyto-vertical distribution to describe the distribution of birds in any vegetation formation. He cited various examples of how ornithologists had defined the vertical zones in different vegetation and which birds occurred within these zones. Over the intervening 65 yr, ornithologists have quantified the vertical patterns of birds (MacArthur and MacArthur 1961, Anderson et al. 1979, Morrison et al. 1990). The vertical occurrence of bird species provides clues to the importance of vegetation structure, and provides a framework for more in-depth studies of avian biology and ecology.

Within the Pacific Northwest of North America, tree species composition (particularly broadleaf versus conifer), gaps, vegetation cover, canopy height, snags, branch architecture, bark texture, foliage type, arrangement and density, and stand age are important attributes for habitat selection by birds in natural forests (Sharpe 1996). Old-growth conifer forests are particularly important, because old growth trees have distinctive crown form, with well-developed branch structure, dead branches and tops, and epiphytic communities (Clement and Shaw 1999, McCune et al. 2000) that contribute to a complex and vertically organized food web (Carroll 1980). Nesting avian species that are known to have their greatest abundance in old-growth forests include hairy woodpecker (*Picoides villosus*), red-breasted sapsucker (*Sphyrapicus rubber*), pileated woodpecker (*Dryocopus pileatus*), Pacific-slope flycatcher (*Empidonax difficilis*), olive-sided flycatcher (*Contopus borealis*), red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes troglodytes*), brown creeper (*Certhia americana*), chestnut-backed chickadee (*Poecile rufescens*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), red crossbill (*Loxia curvirostra*), evening grosbeak (*Coccothraustes vespertinus*), and Vaux's swift (*Caetura vauxi*).

Food resources and structure of temperate hardwood (broadleaf) forests differ from temperate conifer forests, which influences avian composition, use, and vertical occurrence (Jackson 1979, Sabo and Holmes 1983, Sharpe 1996). Conifers produce seed crops favored by nuthatches (*Sitta*), siskins (*Carduelis*), and crossbills (*Loxia*), whereas hardwood forests produce fruits and nuts favored by waxwings (*Bombycilla*), tanagers (*Piranga*),

[1]Author to whom correspondence should be addressed. E-mail: dshaw@u.washington.edu

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and thrushes (*Catharus, Turdus*) (Sharpe 1996). Conifer trees tend to have an excurrent crown architecture with a single main stem (Oliver and Larsen 1990), and the upper canopy becomes an aggregation of spire or columnar tops, separated in space, with age. Hardwood trees, on the other hand, generally have a more decurrent crown architecture with multiple stems in the upper crown (Oliver and Larsen 1990). This results in spreading crowns that are largest near the tops, and the upper canopy of hardwood forests can form a closed forest canopy due to the intersections of these crowns. Young conifer forests may also have a closed upper canopy, but old-growth Douglas-fir (*Pseudotsuga menziesii*) forests generally have an open upper canopy (Parker et al. 2002).

Within old-growth Douglas-fir forests the lower canopy encompasses the dim light zone (Parker 1997) and includes important resources such as the forest floor and soil, down logs, understory vegetation including berry and seed producing shrubs, lower boles of trees and snags, and all the associated arthropods that emerge from soil and forest floor. The mid canopy environment is within the transition light zone of Parker (1997), well above the understory vegetation, and foliage of shade tolerant species such as western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) is concentrated here (Parker 2002). Tree and snag boles, dead branches, heart rot of live trees, and intra canopy gaps are important structural elements. The upper canopy is in the bright light zone of Parker (1997), and is composed of the tops of the dominant and co-dominant tree cohort (Figure 1). Douglas-fir foliage predominates. Most of the conifer seed cones occur in this zone. There is extensive heart and top- rot, many dead tops, double tops, snags, and dead branches that provide habitat for cavity nesting birds and roosting birds, and food resources for wood foraging birds.

Old-growth Douglas-fir forests of the southern Washington Cascades are important winter habitat for resident birds (Manuwal and Huff 1987, Huff et al. 1991). Bark insectivores, timber foliage insectivores, low understory herbivore-insectivores, and timber seed-eaters are more abundant in old-growth than young and mid seral stages of Douglas-fir forests during winter (Huff et al. 1991). Characteristics of old-growth Doulgas-fir forests that may account for this are more reliable cone crop due to higher conifer species diversity, higher density of western hemlock, which is preferred by some foliage insectivores in winter and has a more regular cone crop, higher den-

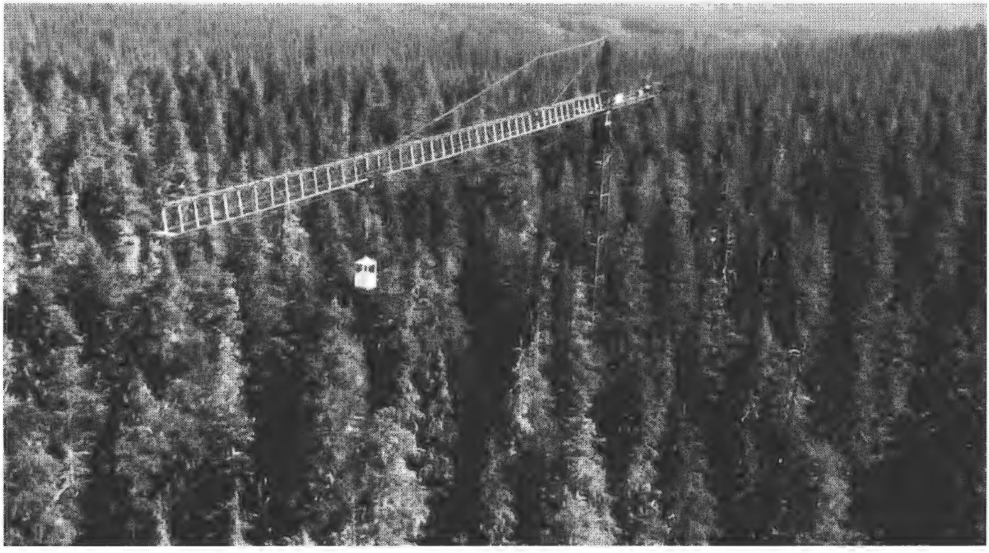

Figure 1. Photograph of the Wind River Canopy Crane, T. T. Munger Research Natural Area, Wind River Experimental Forest, near Carson, Washington. View is looking northeast, and includes old-growth forest surrounding the canopy crane and ~ 75 year-old forest in the background. Photo by Jerry F. Franklin.

sity and larger snags, and higher density of large diameter (>100 cm dbh) live trees.

Most research in vertical aspects of bird assemblages focus on foraging (Sabo and Holmes 1983, Airola and Barrett 1985, Morrison et al. 1990) and this is often limited to a small subset of the avian assemblage, such as cavity nesters (Lundquist and Manuwal 1990, Weikel and Hayes 1999). One study that took a broader perspective considered four eastern North American temperate forest stands in Tennessee and provided data that include vertical distribution (Anderson et al. 1979). About 40% of the avian activity was at the ground level, and the remainder of the activity was distributed uniformly through the canopy.

Old-growth Douglas-fir forests of the Pacific Northwest, with tall stature and complex vertical vegetation structure, provide challenges and opportunities for those who wish to observe birds in the mid and upper canopy strata. Research on the vertical organization of avifauna in these 50+ m forests is generally limited to studies by Lundquist and Manuwal (1990) on four resident cavity nesting species in 48 stands of young and old forests, and Shaw and Flick (1999) using a canopy crane for five resident species in one old-growth stand. Lundquist and Manuwal (1990) organized their observations of vertical foraging locations around individual tree crowns (upper crown, mid crown, lower crown, below crown, no limbs, logs), while Shaw and Flick (1999) organized their observations of vertical occurrence on whole forest canopy zones (upper, mid, and lower).

Lundquist and Manuwal (1990) found that brown creepers were most common in the below crown region, and this remained similar during spring and winter. Chestnut-backed chickadees were common throughout the crowns, slightly more common in the upper crown during winter, but generally similar between seasons. The hairy woodpecker was most abundant in the below crown area, with subtle seasonal shifts, and the red-breasted nuthatch was most abundant in the upper and mid-crown area in spring, with a distinct downward and inward shift in winter.

Shaw and Flick (1999) found the red crossbill was almost exclusively limited to the upper canopy, and this remained relatively constant throughout the year with some occurrence in the mid canopy in spring. The winter wren was limited to the lower canopy all seasons. The brown creeper and golden-crowned kinglet (*Regulus satrapa*) occurred throughout the canopy, but were most abundant in the mid canopy, and this remained so throughout the year. The chestnut-backed chickadee was most abundant in the upper canopy during spring and autumn, and most abundant in the mid-canopy during summer and winter.

Our objectives were to characterize the vertical occurrence of the small bird assemblage in a tall stature old-growth Douglas-fir forest stand. Previous work (Shaw and Flick 1999) using 2 yr of data (included in this study) indicated that five resident species are stratified in the canopy, and this stratification may shift with the seasons. This study focuses on 20 species, includes 3 yr of data, and attempts a more assemblage-wide analysis. We hypothesized that diurnal small birds will be stratified within the canopy, and that each species would be unevenly distributed within the canopy. In addition, we also asked whether these patterns shifted with seasons and whether the patterns we observed in this old-growth forest were similar to those reported for other temperate forests.

Study Site

In 1995, a construction crane was installed in a 60+ m tall old-growth Douglas-fir-western hemlock forest in the southern Cascades, Washington, for use as a forest canopy observatory. The Wind River Canopy Crane (Figure 1) provides access to the entire vertical spectrum of the forest canopy. The crane jib (75 m) is 11.5 m above the tallest tree (63.5 m) and researchers can be lowered into the canopy in a gondola. The canopy crane was used to survey avian occurrence throughout the vertical profile of an old-growth forest stand. A major limitation in this approach is that only one forest stand is sampled. Therefore, any implications for forests in general will require further investigation.

The study site is a ~4 ha forest stand located at the Wind River Canopy Crane Research Facility (http://depts.washington.edu/wrccrf) in the T. T. Munger Research Natural Area (478 ha), Wind River Experimental Forest, near Carson, Washington at 371 m elevation. Mean annual precipitation is 247 cm, however, June, July and August receive only 5% of this total. Mean temperatures are 8.7°C annually, 17.0°C in July, and 0.0°C January. Snowfall averages 233 cm. The site is in the transient snow zone, where snowpack

may not occur for the entire winter. Rain-on-snow, freezing rain, and high winds are common in winter (Franklin 1972).

The forest is a 500-yr old Douglas fir-western hemlock stand (Franklin 1972, Franklin and Dyrness 1988) with a significant component of western redcedar, Pacific yew (*Taxus brevifolia*), grand fir (*Abies grandis*), and Pacific silver fir (*Abies amabilis*). Total density of trees >5 cm diameter at breast height is 429 trees/ha, and basal area is 82.9 m^2/ha. Douglas-fir dominates the stand in height and basal area (35.0 m^2/ha), however, western hemlock dominates in density (224.0/ha >5cm dbh), and amount of foliage. The understory is dominated by vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), Alaska huckleberry (*Vaccinium alaskaense*), red huckleberry (*Vaccinium parvifolium*), and a variety of herbs, ferns, and bryophytes. Graminoids are rare. Coarse woody debris and snags are a significant component of the site.

The vertical structure of the forest is reflected in the light environment, which has been classified into three distinct zones: a lower dim zone to 12 meters, a mid canopy transition zone to 40 meters, and an upper canopy bright zone above 40 meters (Parker 1997). Leaf area has been estimated at 8.6 m^2/m^2, with about 20% of this in understory species (Thomas and Winner 2000). Maximum vertical structure occurs between 15 and 30 m, just above the dim zone (Parker 1997, Song 1998). The vertical structure also reflects the vertical organization of tree species (Song 1998, Ishii et al. 2000). Douglas fir, a shade intolerant species, dominates in the bright zone, which is composed of isolated crowns and groups of crowns with less foliage density in lower levels (Figure 1). The transition zone reflects the increasing abundance of western hemlock foliage, a shade tolerant species, with a few hemlocks reaching 50+ m. The shade tolerant western redcedar is most abundant in the transition and dim zone, with some tree tops reaching 50 m. Pacific silver fir, a shade tolerant species, predominates in the dim zone, especially in canopy gaps. Grand fir is less abundant, but has a higher percentage of trees reaching the bright zone.

The canopy supports over 2 metric tons/ha of epiphytic bryophytes and lichens that are vertically organized. The bryophytes dominate the dim light zone to about 15 m, the lower transition zone is dominated by cyanolichens to about 30 m, and the upper transition zone and bright zone is dominated by alectoriod and non-cyanolichens (McCune et al. 1997). The upper 2 m of the forest, particularly the dead tops of trees, have a unique community of lichens, which may be related to bird roosting, nutrient contributions, and transport of lichen propagules (McCune et al. 2000). The epiphytes reflect the changing microclimate conditions of the vertical profile of the forest. The upper canopy receives more light, UV exposure, greater amounts and speeds of wind, wider extremes of temperature and humidity, and generally more exposed conditions than the protected understory of the dim zone (Geiger 1965, Parker 1995).

The size and location of the Research Natural Area (RNA) and the landscape characteristics of the surrounding region, particularly an adjacent agricultural field, may affect the avian assemblages. No buffer exists against the agricultural edge 500 m south of the canopy crane. For this forest edge, effects of higher temperature, wind, and light, and lower humidity all attenuate individually (Chen et al. 1992, 1993). Maximum distance of the edge effect was about 200 m, leaving about 300 m of interior forest to the south of the crane site. Five hundred meters to the north of the crane site is a 75-yr old, logged and naturally regenerated Douglas-fir forest that was commercially thinned in 1993-1995, leaving a 50 m buffer of young forest on the edge of the RNA. To the east is a wetland about 350 m away. To the west is unbroken old-growth forest for about 1.5 km.

We observed European starling (*Sturnus vulgaris*) and common nighthawk (*Chordeiles minor*) in the open fields. The European starling nests in the old growth trees along the field edge, and in the buildings at the south end of the field. They feed in the fields, often in small flocks. They began attempting to nest on the crane in the second year (1997) after it was erected. We controlled the occurrence of these birds by shooting about 9-12 individuals each year. The common nighthawks nest in adjacent fields and feed over old growth. The birds consistently foraged over the old-growth, but did not exclusively use this habitat for foraging.

Methods

Field Methods

We took a simplistic approach to the vertical occurrence of birds by dividing the canopy into three

equal zones. These zones reasonably reflect vertical forest structure differences that create the dim, transition, and bright light zone of Parker (1997). We then sampled these vertical zones weekly for 3 yr, by using fixed area point counts (Hutto et al. 1986, Manuwal and Carey 1991) from the gondola of the canopy crane to determine relative differences in composition and abundance of birds. Fixed-area point counts are generally used to compare the relative abundance of birds among sites such as young, mature, and old-growth forests (Manuwal 1991). In this case, we used the technique to describe the relative abundance of birds within three canopy strata of a tall forest stand.

A total of 121 surveys were conducted weekly from 21 March 1996 until 21 March 1999, averaging 40/yr. The canopy was divided in three vertical zones: lower canopy (0-20 m), mid canopy (21-40 m), and the upper canopy (41 m to under the jib of the crane, which varies from 69 m to 75 m with slope). Thirty-meter radius point count plots were conducted from the gondola at 10 m, 30 m, and 50 m, at approximately the mid-points of each canopy level. All birds seen or heard in the plot were noted during a 5 min period following a 3 min quiet down. The vertical series of plots was replicated in the four cardinal directions. Therefore, four point count plots were located in each canopy zone. Each vertical plot series was located 85 m horizontally from the tower of the crane, making the center of each plot series 120 m from the nearest plot series.

With only a 3-min quiet down between vertical plots, in a sequence of top to bottom, it is possible we counted the same bird more than once. Because the purpose of this study was to determine the relative occurrence of species by zone, the repeat counts do not matter. We only wanted to know whether a zone was used by a particular species of bird.

The totals from each canopy level were summed for each day, therefore the data represent 20 min of survey from each canopy level. Surveys began within 30 min of dawn, except from mid November through February when the surveys began during mid morning. Total time to complete the entire 12 survey plots took ~ 2.5 hr. Surveys were not conducted during snowfall, rainfall, high winds, or if lightning or thunder were detected. In addition, no other personnel were allowed on the site before or during avian surveys. The 30 m radius plot size was designed to insure that all birds in the plots were detected, because identifications can be especially difficult during the non-breeding season (Best 1981).

Caveats of Using a Crane to Sample the Avian Community

Although the canopy crane provides access to observe the avian community, some aspects of the canopy crane may negatively affect the birds. General use of the site by people may influence the avian assemblage and its use of the canopy (Gurtzwiller et al. 1994, 1998). Minor noises are associated with operation of the crane, including an electrical transformer at the base 85 m from the point count plots, cooling fans on motors at the rear of the counterbalance jib 110 m from the point count plots, and a cooling fan on the trolly motor directly above the position of the gondola on the jib.

Each morning, prior to using the crane, a test lift is required by law. The gondola is lowered to the ground and inspected, at which time a test weight is attached to the gondola and the gondola is lifted back up to the highest possible point (67 m) to test a limit switch. The gondola is moved out to the end of the jib at 85 m, the jib is swung in a complete 360° revolution over the stand, then the gondola is lowered to the ground. This inspection and test lift takes about 45 min. Therefore, if dawn is at 0500 and the survey begins at 0515, then the test lift begins at 0430. Swinging the jib over the stand definitely affects birds in the upper canopy, but our attempts to quantify this effect have remained unsuccessful. In general, smaller birds seem to be less affected than larger birds.

Analysis: Vertical Occurrence

The 20 most abundant species detected in vertical plots were used for analysis of vertical patterns. A Chi-square Goodness of Fit test (Zar 1999) was applied to test if their distribution among the three canopy levels was significantly different from random. The null hypothesis was that birds are equally distributed within the three canopy zones. The term stratified is used to describe the distribution of birds that are not equally distributed within the canopy. Finally, a proportional bar chart for the 20 most abundant species illustrated the vertical occurrence and the proportion of the total detections in each of the canopy zones.

Analysis: Seasonality of Vertical Patterns

We defined seasons of the year based on weather and occurrence of birds for this site, and designated three seasons: early (March - June, total surveys = 42), late (July - October, total surveys = 46), and winter (November - February, total surveys = 33). The six resident species with counts of at least four in each of the three seasons were examined by use of proportional bar charts that helped evaluate how their distribution throughout the canopy changed with the seasons. These seasonal changes were further investigated with Analysis of Deviance, using a Poisson Error Structure and a Log link (Mathsoft 1998), which was used in an earlier analysis of five resident species (Shaw and Flick 1999). This particular regression method was chosen because of the count data structure. Histograms of the counts for each species revealed that counts were distributed with a high proportion of zeros and a long right tail, characteristic of Poisson Data. The main effects of season and level indicate if bird occurrence is evenly distributed over the year and over the canopy levels. The interaction term indicates whether the vertical distribution of the species changes with the seasons. Although no additional statistics were used, proportional charts were used to display the change in canopy use of the total number of birds detected in each zone.

Results

Vertical Occurrence of Species

Twenty-nine species of birds were detected in the fixed-area observation plots (Table 1). The most species, greatest number of guilds, and greatest

TABLE 1. Species list of birds detected in 30 m radius fixed-area observation plots during 121 surveys from March 21, 1996 to March 21 1999 at the Wind River Canopy Crane Research Facility. Code is the four letter species codes used in figures. Guilds codes are based on Manuwal (1991) and general literature: AI - Air insectivore, BI - Bark insectivore, LUHI - Low understory herbivore-insectivore, N - Nectarivore, OFGF - Open field ground feeder, OS - Omnivore-scavenger, TFI - Timber foliage insectivore, TFIO - Timber foliage insectivore-omnivore, TS - Timber seed-eater. Migration: NM = neotropical migrant, RM = regional migrant, R = resident. *not included in analysis because of insufficient detections in fixed radius plots.

Species	Scientific name	Code	Guild	Migration
Common nighthawk	*Chordeiles minor*	CONI	AI	NM
Vaux's swift	*Chaetura vauxi*	VASW	AI	NM
Rufous hummingbird*	*Selasphorus rufus*	RUHU	N	NM
Red-breasted sapsucker	*Sphyrapicus rubber*	RBSA	BI	RM
Hairy woodpecker	*Picoides villosus*	HAWO	BI	R
Northern flicker*	*Colaptes auratus*	NOFL	BI	RM
Pacific-slope flycatcher	*Empidonax difficilis*	PSFL	AI	NM
Gray jay	*Perisoreus canadensis*	GRJA	OS	R
Steller's jay	*Cyanocitta stelleri*	STJA	OS	R
Violet-green swallow*	*Tachycineta thalassina*	VGSW	AI	NM
Chestnut-backed chickadee	*Poecile rufescens*	CBCH	TFI	R
Red-breasted nuthatch	*Sitta canadensis*	RBNU	BI	R
Brown creeper	*Certhia Americana*	BRCR	BI	R
Winter wren	*Troglodytes troglodytes*	WIWR	LUHI	R
Golden-crowned kinglet	*Regulus satrapa*	GCKI	TFI	R
Ruby-crowned kinglet*	*Regulus calendula*	RCKI	TFI	RM
Swainson's thrush*	*Catharus ustulatus*	SWTH	LUHI	NM
Hermit thrush	*Catharus guttatus*	HETH	LUHI	NM
American robin	*Turdus migratorius*	AMRO	LUHI	RM
Varied thrush	*Ixoreus naevius*	VATH	LUHI	RM
European starling	*Sturnus vulgaris*	EUST	OFGF	RM
Hermit warbler	*Dendroica occidentalis*	HEWA	TFI	NM
Western tanager*	*Piranga ludoviciana*	WETA	TFI	NM
Chipping sparrow*	*Spizella passerina*	CHSP	OFGF	NM
Dark-eyed junco	*Junco hyemalis*	DEJU	LUHI	RM
Black-headed grosbeak*	*Pheucticus melanocephalus*	BHGR	TFIO	NM
Red crossbill	*Loxia curvirostra*	RECR	TS	R
Pine siskin	*Carduelis pinus*	PISI	TS	RM
Evening grosbeak*	*Coccothraustes vespertinus*	EVGR	TS	NM

number of total bird detections were documented in the upper canopy (Figure 2). A few species in each zone accounted for most of the observations (Figure 3). For example, the chestnut-backed chickadee accounted for 41% of the birds in the mid canopy and 38% of the birds detected in the upper canopy. In the lower canopy, the five most abundant species were more evenly distributed (Figure 3).

Fifteen of the 20 most common species were significantly more abundant in one level of the canopy (Table 2). The distributions of air insectivores, timber foliage insectivores, and timber seed eaters were stratified within the canopy, as were most of the low understory-herbivore-insectivores. The bark insectivores, except the brown creeper, and omnivore-scavengers, except gray jay (*Perisoreus canadensis*), were not stratified within the canopy. However, the absence of a detected canopy preference for the red-breasted sapsucker, hairy woodpecker, Steller's jay (*Cyanocitta stelleri*), and

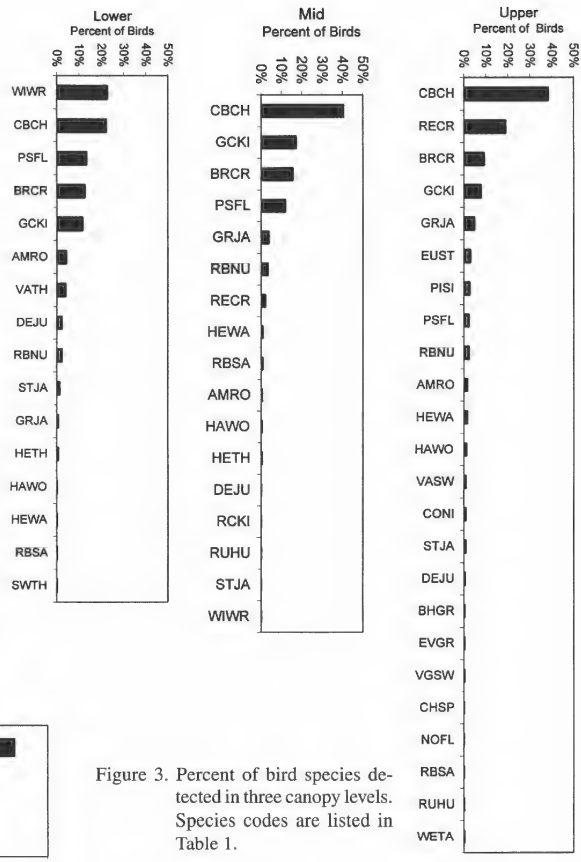

Figure 3. Percent of bird species detected in three canopy levels. Species codes are listed in Table 1.

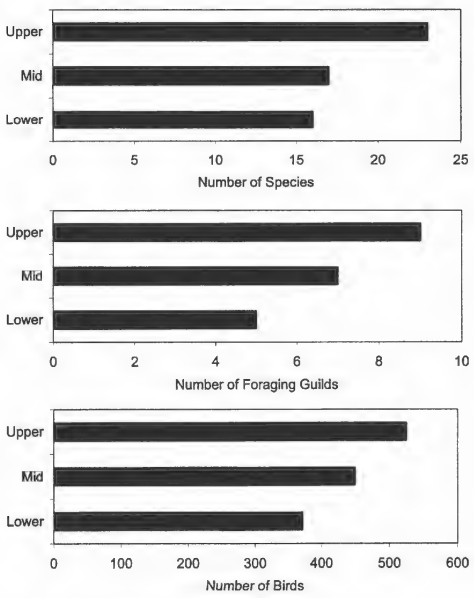

Figure 2. Distribution of number of species (A), number of foraging guilds (B), number of birds (C), in the low, mid, and upper canopy.

hermit thrush, may be a function of a small sample size (Table 2).

The forest stand was vertically used (Figure 4), with some species detected exclusively in the lower canopy, some only in the upper canopy, and some throughout the canopy. Species detected exclusively in the upper canopy were common nighthawk, Vaux's swift, European starling, and pine siskin (*Carduelis pinus*), whereas species most prevalent in the upper canopy were the hairy woodpecker, gray jay, red crossbill, hermit warbler (*Dendroica occidentalis*), and chestnut-backed chickadee (Table 2, Figure 4). The Pacific-slope flycatcher was most prevalent in the mid and lower canopy, the red-breasted nuthatch was most prevalent in the mid and upper canopy, whereas the red-breasted sapsucker, brown creeper, and golden-crowned kinglet were mostly detected in the mid

TABLE 2. Chi-square Goodness-of-Fit test to determine whether birds were evenly distributed in the three canopy levels, for the twenty most abundant birds in the research forest.

Species	Number of birds Lower	Mid	Upper	Total	*P*
Unevenly distributed ($P \leq 0.05$)					
Common nighthawk	0	0	5	5	0.01
Vaux's swift	0	0	6	6	0.00
Pacific-slope flycatcher	50	54	13	117	0.00
Gray jay	3	17	26	46	0.00
Chestnut-backed chickadee	83	183	208	474	0.00
Brown creeper	47	71	49	167	0.04
Winter wren	85	1	0	86	0.00
Golden-crowned kinglet	43	78	42	163	0.00
American robin	16	3	9	28	0.01
Varied thrush	15	0	0	15	0.00
European starling	0	0	16	16	0.00
Hermit warbler	1	4	9	14	0.03
Dark-eyed junco	9	1	4	14	0.03
Red crossbill	0	10	103	113	0.00
Pine siskin	0	0	15	15	0.00
Evenly distributed ($P > 0.05$)					
Red-breasted sapsucker	1	4	1	6	0.22
Hairy woodpecker	1	3	7	11	0.08
Red-breasted nuthatch	9	15	13	37	0.47
Steller's jay	5	1	5	11	0.23
Hermit thrush	3	3	0	6	0.22

canopy (Table 2, Figure 4). The winter wren and varied thrush were detected in the lower canopy, while the hermit thrush was detected only in the lower and mid canopy. Finally, the Steller's jay, dark-eyed junco (*Junco hyemalis*), and American robin (*Turdus migratorius*) were prevalent in the lower and upper canopy, but not in the mid canopy (Table 2, Figure 4). The sum of the three timber foliage insectivores (chestnut-backed chickadee, golden-crowned kinglet, hermit warbler) is highest for the mid canopy and upper canopy (low - 127, mid - 265, upper - 259), as well as the sum of the four bark insectivores (brown creeper, red-

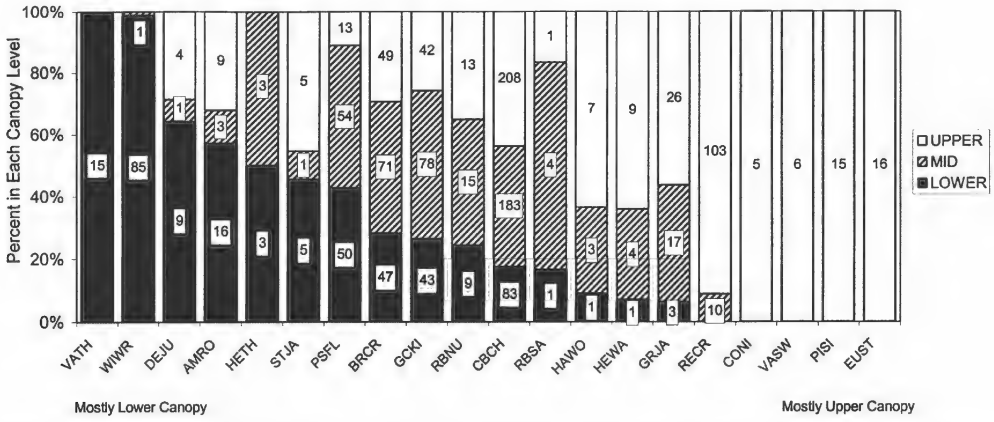

Figure 4. Proportional detections (percent of total) for of low, mid and upper canopy by twenty most abundant bird species. Species codes are listed in Table 1.

breasted nuthatch, hairy woodpecker, red-breasted sapsucker) (low - 58, mid - 93, upper - 70).

Seasonality of Vertical Patterns

All six resident species were most abundant at one canopy level during each season, but the particular canopy level shifted for four of the species (Table 3, Figure 5). The brown creeper shifted downward in the winter. The red crossbill, chestnut-backed chickadee, and gray jay shifted upward

TABLE 3. *P* values for differences among canopy levels, seasons and the interaction for the six most common year round residents.

Species	Canopy Level	Season	Canopy/Season Interaction
Gray jay	0.00	0.46	0.04
Chestnut-backed chickadee	0.00	0.00	0.00
Brown creeper	0.05	0.00	0.00
Winter wren	0.00	0.00	0.80
Golden-crowned kinglet	0.00	0.00	0.07
Red crossbill	0.00	0.00	0.00

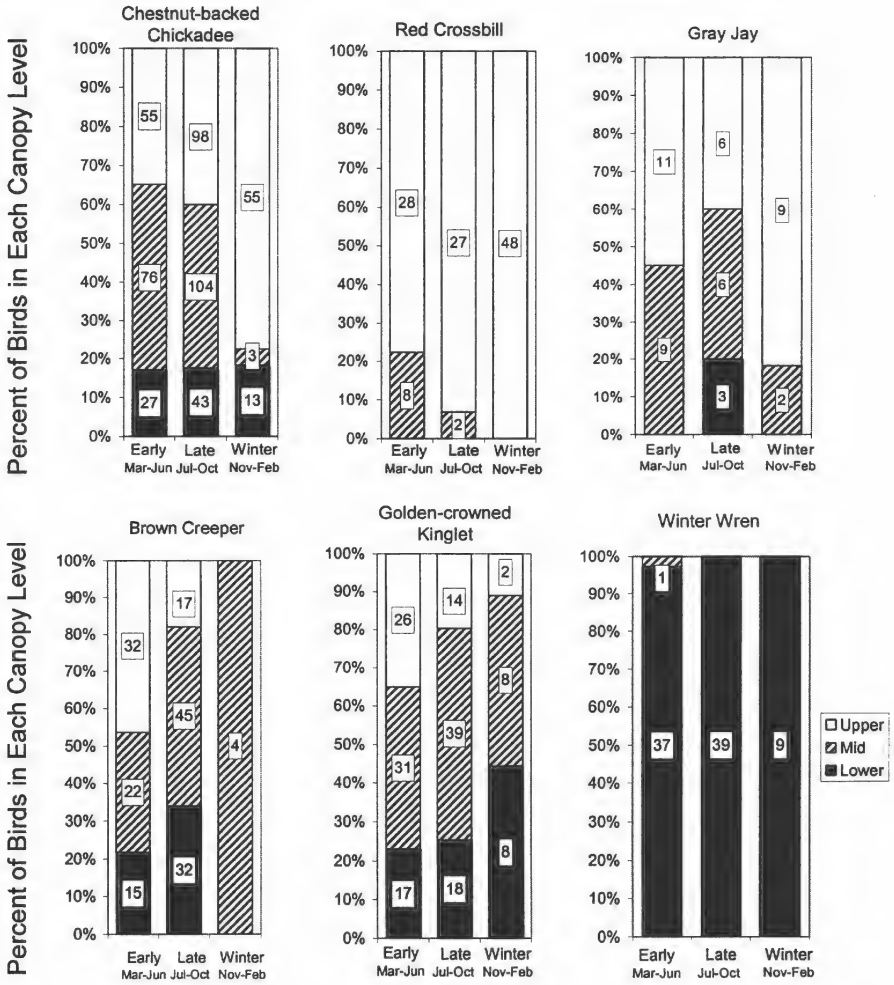

Figure 5. Proportional detections within the canopy during three seasons, early (March-June), late (July-October), and winter (November-February) by the six most abundant year-round residents.

during the winter. The winter wren was only detected outside the lower canopy zone once in a western redcedar tree at ~24 m (4 m above the zone division).

Three species had residual deviance larger than their residual degrees of freedom in the analysis of deviance, indicating over dispersion. This could be caused by an aggregated spatial distribution. These three species, chestnut-backed chickadee, golden-crowned kinglet, and red crossbill were often observed in flocks, especially outside the breeding season. The independence assumption is violated, and therefore the *P* values should be used only as general guidelines.

The total number of birds detected in each zone also shifted with the seasons (Figure 6). During the early season the mid and upper canopy were about equal with somewhat fewer birds detected in the lower canopy. During the late season detections were generally equal through the three canopy zones. However, there was a sharp shift upward during the winter, and a general lack of detections in the mid canopy.

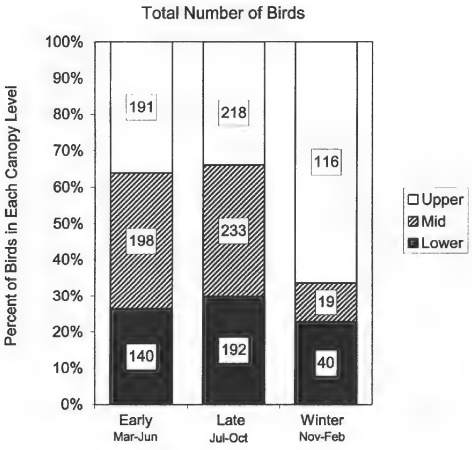

Figure 6. Proportional distribution of detection totals of birds within the three canopy levels by three seasons; early (March-June), late (July-October), and winter (November-February).

Discussion

The diurnal small bird assemblage of the Wind River old-growth was characteristic of this forest type in the southern Washington Cascade Range (Manuwal 1991, Huff and Raley 1991, Huff et al. 1991, Lundquist and Mariani 1991), except for the European starling, which was attracted to the crane from the nearby (500 m) nursery fields. The small bird assemblage at Wind River was dominated by residents and regional migrants, with five (25%) common neotropical migrants present during May through August, a proportion similar to that noted by MacArthur (1959) for western Oregon forests in general. In northeastern forests (Sabo and Holmes 1983) and Sierran forests (Airola and Barrett 1985) of North America the resident species tend to exploit food resources that reflect winter feeding, such as arthropods on tree boles, twigs, and conifer foliage (and at Wind River, conifer seed), whereas the neotropical migrants tend to occupy more seasonal niches such as aerial (at Wind River: Vaux's swift, common nighthawk, Pacific-slope flycatcher), terrestrial (at Wind River: hermit thrush), and foliage (at Wind River: hermit warbler) insectivory.

The majority of birds (15 of 20 species) analyzed in this study were stratified within the canopy (Table 2, Figure 4). This stratification reflects their uneven distribution within the canopy, yet most species occurred throughout the canopy (Figure 3, 4). Canopy zone specialists were most common for the upper canopy. The only species generally restricted to the lower canopy was the winter wren. The varied thrush was not detected above the lower canopy but we have observed birds in the mid and upper canopy outside plot observation periods. None of the avian species was restricted to the mid canopy, although many species were most abundant there and this is a key zone for foliage insectivores and bark insectivores. Five species were generally restricted to the upper canopy in this stand, including common nighthawk, Vaux's swift, European starling, pine siskin, and red crossbill. The Vaux's swift nests and roosts in the old-growth, feeds in the upper canopy in mornings, but was often observed over fields and other forests, and very high above ground during later times of day. The pine siskin and red crossbill are wide ranging birds, using the old-growth forest for feeding and perhaps nesting.

The vertical occurrence of birds is reflected in the vertical structure of this old-growth forest stand. The moss dominated, dim light zone of the lower canopy, with berry producing shrubs, is characterized by low understory herbivore insectivores such as the winter wren, American robin, varied thrush, and dark-eyed junco (Figure 4).

However, the chestnut-backed chickadee, Pacific-slope flycatcher, golden-crowned kinglet and brown creeper were among the most commonly observed birds there (Figure 3), perhaps due to the abundance of conifer and vine maple foliage, deeply crevassed lower Douglas-fir boles, and flying insects. The mid canopy has the highest density of conifer foliage, and is characterized by foliage insectivores and bark insectivores (Figure 4). The Pacific-slope flycatcher was also abundant in this zone. This flycatcher was not commonly observed foraging in a classic sally-aerial flycatcher move, but mostly observed as a hyperactive, within crown forager, constantly moving among branches, epiphytes, and foliage. The upper canopy structure was open, with much space between tree crowns, dominated by Douglas fir, and characterized by dead wood and lichens. We detected the most hairy woodpeckers in this zone (Figure 4), although Lundquist and Manuwal (1990) detected hairy woodpeckers most commonly in the below crown zone. The greatest number of birds, and greatest diversity of species and guilds (Figure 2) were detected in the upper canopy, while aerial insectivores, timber seed eaters, foliage insectivores, and bark insectivores characterized the avian assemblage (Figure 3, 4). The complex and varied upper canopy of this old-growth forest is an important forest strata for biological diversity which has been little studied.

Of the six bird species examined for seasonal shifts in vertical occurrence in this study, the winter wren and golden-crowned kinglet did not shift zones with the seasons, whereas the chestnut-backed chickadee, red crossbill, and gray jay all shifted the bulk of their activity to the upper canopy, and the brown creeper was detected exclusively in the mid canopy. This compares to Lundquist and Manuwal (1990) who studied foraging locations and found chestnut-backed chickadees remained high in the canopy, red-breasted nuthatch shifted inward and downward, and hairy woodpecker and brown creeper did not shift vertical position of foraging during winter. Shaw and Flick (1999) used all four seasons to compare vertical occurrence and found chestnut-backed chickadees were most abundant in the upper canopy during spring and autumn, and most abundant in the mid-canopy during summer and winter.

In the Wind River forest, the total number of birds detected, as a percent of the total detections, shifted to the upper canopy in winter (Figure 6). The upper canopy may have more resources such as cavities, sun warmed foliage and tree boles, arthropods, and conifer seed, while the microclimate may be less severe during the day than the snow covered, humid understory. However, severe weather is known to depress the vertical foraging patterns of birds in winter (Grubb (1975, 1977), and we surveyed birds only on days with no rain, snow, or high winds. Therefore, we only have a snapshot of vertical occurrence on the more favorable winter days.

At Wind River, 4 of the species (20%) were detected most often in the lower canopy, 5 species (25%) in the mid canopy, 9 species (45%) in the upper canopy, while 1 species (5%) was equal in the low and mid canopy, and 1 species was equal in the low and upper canopy (Table 2). Sabo and Holmes (1983) provide data on mean height of foraging activity for woodpeckers and insectivorous birds in a northern hardwood forest (mean tree height 22 m) and a subalpine conifer forest (mean tree height 7 m). We divided the forest studied by Sabo and Holmes (1983) into thirds and determined the number of birds whose mean foraging height corresponded to low, mid, and upper canopy environments. Within the northern hardwood forest, 8 species (36%) had mean foraging heights in the lower canopy, 14 species (64%) in the mid canopy and 0 in the upper canopy. Within the subalpine conifer forest, 4 species (20%) had mean foraging heights in the lower canopy, 7 species (35%) in the mid canopy, and 9 species (45%) in the upper canopy. In the hardwood forests studied by Anderson et al. (1979), 40% of the avian occurrence was near the forest floor, and the remaining activity was evenly distributed through the canopy.

Although these three studies are a small sample size for comparisons, the vertical distribution of small birds in conifer forests appears to be skewed to the mid-upper canopy, bird distribution in hardwood forests tends to be skewed to the mid-lower canopy. A variety of factors is obviously involved, but the characteristic structural and resource differences between hardwood and conifer forests may play a leading role. The forest floor and soils in hardwood forests is generally more basic, and supports larger arthropods and earthworms, while the acidic soils and forest floor of conifer forests supports mites and smaller arthropods. The larger fruits and nuts of hardwood forests fall to the forest floor, where they, and their associated arthropods,

may be fed on by low understory herbivore insectivores. This may increase the number of forest floor feeding birds in hardwoods as compared to conifer stands. The upper canopy of conifer forests is more open, and may be more suitable for a wider range of foraging guilds that move among and between the tree-tops and along the large main stems, than the upper canopy of hardwood forests. Temperate zone hardwood forests, on the other hand, with a closed forest upper canopy and small branches, have fewer foraging guilds in the upper canopy, decreasing the number of upper canopy birds relative to conifer forests.

In this tall stature old-growth forest, the vertical development of canopy structure provides a diversity of habitat elements and microclimate conditions, which are key to vertical canopy use by birds. This general relationship of bird species diversity and forest height diversity is well known in forest-avian research (Dunlavy 1935, MacArthur and MacArthur 1961, Willson 1974). However, the structure of the upper canopy of this old-growth forest leads to avian specialists occurring there in the breeding season, and the relative proportion of resident birds in the upper canopy increases in winter. The complex structure of old-growth Douglas-fir forests, particularly the upper canopy, is unique and important, requiring further vertically organized study to validate results from this single site research.

Acknowledgements

This research was supported by the Wind River Canopy Crane Research Facility, a cooperative scientific endeavor of the University of Washington, College of Forest Resources, US Forest Service, Pacific Northwest Research Station, and Gifford Pinchot National Forest. Special thanks to Mark Creighton, research tower crane operator. Thanks to an anonymous reviewer and Michael Morrison for comments on an earlier version of this manuscript.

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Received 21 August 2001
Accepted for publication 28 May 2002

F. Louise Waterhouse[1], Research, Vancouver Forest Region, British Columbia Ministry of Forests, 2100 Labieux Road, Nanaimo, British Columbia V9T 6E9

Alton S. Harestad, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6

and

Peter K. Ott, Research Branch, British Columbia Ministry of Forests, P.O. Box 9519, Stn Prov Govt, 712 Yates Street, Victoria, British Columbia V8W 9C2

Use of Small Streams and Forest Gaps for Breeding Habitats by Winter Wrens in Coastal British Columbia

Abstract

Few studies have examined the value of riparian areas adjacent to streams ≤ 10-m wide as habitat for forest birds. In mature (80-120 yr) and young (40-60 yr) coastal forests of southern British Columbia, we examined the habitat values for male winter wrens of riparian areas adjacent to small streams and areas upslope of these streams. In both riparian and upslope areas, wrens preferentially located nests (n = 47) and song perches (n = 77) in disturbed sites with fewer trees than randomly located sites. Hydrological processes associated with streams, mortality of dominant canopy trees or uprooted trees can produce these disturbed sites. In mature forest, winter wrens chose stream banks and upturned root masses when available for building their nests with most nest substrates located within 5 m of small streams. In both young and mature forests, they also chose areas near small streams as locations for song perches. Winter wrens may use areas closer to streams when available because channel morphology, the associated heterogeneous forest structure, and microclimate likely provide optimal nesting and foraging habitat. Our research supports operational efforts by forest managers to conserve structures near small streams and in upslope areas because these structures maintain long-term habitat values for wildlife such as winter wrens.

Introduction

Riparian habitats provide resources to wildlife that complement those available in forested upslope habitats away from streams (Raedeke 1988). These include water, unique microclimate, and structurally diverse and disturbed sites. Such sites in forests are characterized by complex vertical vegetation structure associated with the riparian forest edge interfaces, and openings in the understory and overstory canopy (Gregory et al. 1991, Voller 1998). Openings in the overstory canopy that result from stream processes are called edaphic gaps (Lertzman et al. 1996). Mortality of standing canopy dominants and uprooted trees, referred to as gapmakers, also produce open and disturbed sites but these are called developmental gaps (Lertzman et al. 1996). Developmental gaps may contribute to the canopy opening above streams and in areas away from streams providing structural heterogeneity in the forest (Spies et al. 1990, Lertzman et al. 1996). Gaps have distinct microclimates in their understory because higher light intensities occur without shading from the overstory canopy. Furthermore, greater amounts of moisture accumulate because the canopy does not intercept rain and fewer roots remove water (Blake and Hoppes 1986, Schaetzl et al. 1989, Shure and Phillips 1991). Uprooting of trees can create pits that flood and drain poorly thereby becoming locally wet sites (Beatty and Stone 1986).

Few studies in the Pacific Northwest of North America have determined for forest birds the importance of riparian habitats of small streams relative to habitats upslope, and how best to manage these riparian habitats (Carey 1988, McGarigal and McComb 1992, Kinley and Newhouse 1997, Hagar 1999). As well, the transition in vegetation composition and structure from riparian areas upslope into the adjacent forest is often subtle in temperate and boreal forest stands, particularly when streams lack floodplains (Gregory et al. 1991, Naiman et al. 1993, Wiebe and Martin 1998). In British Columbia, this subtlety has obscured the need to manage habitats along small streams for terrestrial wildlife. Instead, placement of reserves or management zones is directed toward streams

[1]Author to whom correspondence should be addressed. Email: Louise.Waterhouse@gems1.gov.bc.ca

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that are fish bearing or within community watersheds (B.C. Ministry of Forests and B.C. Ministry of Environment 1995). We therefore studied habitat selection by winter wrens, a common forest insectivore, to improve our understanding on how the forest surrounding small streams can provide habitat for wildlife.

The winter wren is significantly more abundant in old-growth forest compared to 40-80-yr second-growth in the south coast mainland region of British Columbia, but nearly absent from clearcut blocks of < 5-yr since harvest (Savard et al. *in press*). Yet age alone can be a poor criterion for managing habitats for wildlife (Rotenberry and Wiens 1980, Hayes et al. 1997, Waldien et al. 2000). In the Pacific Northwest, winter wrens are more numerous in structurally diverse stands (Carey et al. 1991, Hansen et al. 1995) and associated with riparian habitats (Barrows 1986, McGarigal and McComb 1992, Kinley and Newhouse 1997). Our main objective was to determine in the drier coastal temperate rainforest whether riparian habitats of small streams (≤ 10 m-wide, including seeps with surface water) are selected by male winter wrens for territories and nesting because of resources that differ from those available in upslope habitats away from streams.

Territories of birds include habitats that can provide food, nest sites, security cover, and shelter (Martin and Roper 1988). As well within these habitats, song perches are used by male winter wrens to advertise and defend their territory, to attract mates, and to advertise potential nests (Armstrong 1956, Garson 1980). Nest sites, as microhabitats within the territory, may be a major factor that influences placement of territories by birds (Matsuoka et al. 1997). Male winter wrens usually weave several nests from moss and twigs within available cavities in their territories (Armstrong 1956, Armstrong and Whitehouse 1977, Wesolowski 1983). Winter wrens in coastal British Columbia raise one or more broods from mid-April to mid-July and some males are polygynous (McLachlin 1983). Long-term habitat needs are important for winter wrens because they are site tenacious and can occupy the same territories in successive years. Streams and canopy gaps may be key criteria used by winter wrens to ensure they place themselves in high quality habitat for nesting or foraging (Fretwell and Lucas 1969, Cody 1981, Orians and Wittenberger 1991, Sodhi et al. 1999).

We used two approaches to study winter wrens. For one approach, we examined differences in habitat use by winter wrens observed in two seral stages. In 1996, we compared microhabitat used by winter wrens at singing locations between young structurally uniform forest (40-60 yr) and mature structurally heterogeneous forest (80-120 yr). We hypothesized that winter wrens should be positively associated with streams in both seral stages if characteristics unique to streams influence the spatial distribution of wrens. However, if streams only provide favorable habitats (e.g., structure) under particular conditions of disturbance history or stage of stand development, then the response of winter wrens to streams would likely differ between seral stages. We expected that the importance of riparian habitat for enhancing stand capability to support terrestrial wildlife such as the winter wren varies among stands, but is likely greater in structurally uniform forests. For our other approach, in the mature forest, we tested during 1995 and 1996 if winter wrens nested (nest substrates and nest sites) closer to small streams when available, and if the occurrence of nesting habitat is an important factor for selection of territories by males.

Study Area

Our study area was along south coastal British Columbia between Roberts Creek and Powell River (49°35'N, 123°38'W; elevation 350 to 550 m). Warm, relatively dry summers, and moist, mild winters, with little snowfall are typical in this region. The study area was mostly within the Coastal Western Hemlock Dry Maritime Subzone (CWHdm), although parts were transitional between the CWHdm and the Coastal Western Hemlock Submontane Very Wet Maritime variant (CWHvm1) (Meidinger and Pojar 1991, Green and Klinka 1994). The CWHdm is dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and lesser amounts of western redcedar (*Thuja plicata*). Douglas-fir is replaced by Pacific silver fir (*Abies amabilis*) in the transitional area. The forest understory is sparse and patchy, dominated by salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), and red huckleberry (*Vaccinium parvifolium*) or with Alaskan blueberry (*Vaccinium alaskaense*) in the transitional area. Streams in our study area were mostly ≤ 10 m-wide on gentle slopes (gradients < 11.5°). Generally, those with channels

5-10 m-wide had water throughout the breeding season, undercut banks along most of their length, gullied topography, and gaps in the overstory canopy along most of the stream course. Streams with channels < 5 m-wide were usually seasonal with sporadic undercut banks and few canopy gaps. Our definition of small streams included seeps with free surface water during the breeding season because sites with moist soils can also differ in stand structure, microclimate and associated plant and insect communities (Wesolowski 1983, Holmes and Robinson 1988, Tobalske et al. 1991, Sohdi et. al. 1999). Over the past century, different forest harvesting regimes were used in our study area. The young forest stands regenerated after clearcut harvesting, whereas the mature forest stands originated after fire but had single tree selection harvesting for large diameter remnant redcedar. The study sites were on Crown Land (Timber Sale License area of the Small Business Forest Enterprise Program, British Columbia Ministry of Forests) and within Block 1 of Tree Farm License 39 of Weyerhaeuser Co. Ltd.

Methods

Winter Wren Sampling

We used two survey methods during the winter wren active breeding season from late April to early June, from sunrise to 4 hr after sunrise (Verner 1985). During 1996, in both young and mature forest, we used transects over the entire study area to locate singing winter wrens and their song perches (wren locations). In randomly selected stands from those accessible to us, we placed 500-m transects, a minimum of 400 m apart and parallel to the contours, to obtain a range of distances from streams ≤ 10 m-wide. We conducted one survey along each transect and flagged all winter wren song perches that were detected within 150-m of either side of the line (our estimated maximum detection distance for winter wrens). If a singing wren moved from its song perch before we located the perch, we estimated its original location within 5 m. For each wren location, we randomly selected and flagged a location on the same transect within the 150-m boundaries. The sample of random locations provided an estimate of habitat available to winter wrens. Our methods did not account for possible non-breeding singing males or for individuals singing away from territories (Haila et al. 1989, Van Horne 1995).

During 1995 and 1996 in five study blocks of a south aspect, mature forest stand located at the Roberts Creek Study Forest, we mapped territories of winter wrens and identified their nest sites and nesting substrates. We randomly selected five streams, 5-10 m-wide, from those available in 1995 then we randomly located and centered on each a 12-ha (400-m-wide x 300-m-long) study block with a 25 x 25-m survey grid. Although centered on a stream 5-10 m-wide each study block included streams < 5 m-wide and seeps. This design facilitated examination of the spatial distribution of territories and nests in relation to streams 5-10 m-wide and < 5 m-wide. We included these < 5 m-wide streams because they are common in coastal forests and differ in structure compared to streams 5-10 m-wide. In 1996, we expanded the study blocks to 27-ha (600-m-wide x 450-m-long). We conducted 16-20 winter wren surveys each year in these study blocks recording all observations (visual, singing and counter-singing, mating displays, and nesting behaviors) (Verner 1985). Our mapping accuracy was improved by capturing (Falls 1981) and banding males in 1995 (24/35 territories) and 1996 (19/45 territories). We used two or three color-coded plastic bands in unique combinations and a numbered aluminum band provided by Environment Canada. During surveys, we located most nests through observations of displaying males or of birds carrying either nesting material or food (Martin and Geupel 1993). In addition, we located nests using searches focused in the vicinity of song perches in territories (Garson 1980). To minimize attracting predators to nests, we flagged 10 m from nests and measured habitat attributes after the young had fledged.

Habitat Measurements

We measured habitat attributes on transects at wren and random locations. Also, we measured habitat attributes at nests and in the five 27-ha study blocks at the 50 x 50-m points (n = 315; 65 per grid) on the 25 x 25-m survey grids. We measured slope and aspect at all sample locations. For wren and random locations, we used 0.20-ha slope-corrected circular plots and estimated percent overstory tree canopy cover (evergreen, deciduous, and combined) for dominant, codominant, intermediate, and total canopy classes. Using 0.01-ha slope-corrected circular plots, we estimated percent cover of herbs, ferns, shrubs

(individually and combined as total understory vegetation), moss, rock, exposed soil, and tree canopy (evergreen, deciduous, combined) in height strata (< 0.5 m, 0.5-< 2.0 m, ≥ 2.0 m, ≥ 0.5 m, and total combined). At nests and 50 x 50-m survey grid points, we used slope-corrected nested circular plots. We measured understory vegetation for the stratum < 0.5 m-high in 0.002-ha plots and we used 0.01-ha plots for overstory canopy cover and understory vegetation in strata ≥ 0.5 m-high and total combined, and to count stems of trees and snags < 10 cm dbh. In addition to the above habitat attributes measured at wren and random locations, we estimated percent cover of deciduous and evergreen shrubs individually and combined, and we estimated percent ground cover (rock and duff). In 0.02-ha plots, we counted stems of trees and snags ≥ 10 cm dbh (Luttermerding et al. 1990) and numbers and types of upturned root masses as prime with loose soil and rootlets for nests or as other. We estimated percent cover of strata using the mean from two visual estimates of the vertical projection of the vegetation (Luttermerding et al. 1990).

To describe horizontal forest structure at all sample locations, we measured distance to the nearest stream (including noticeable seeps), the nearest upturned root mass, and mean distance to overstory canopy and understory canopy (≥ 0.5 m-high) trees and snags (Noon 1981, Morrison et al. 1992). Mean distance was calculated using a plotless method. Each location was divided into four 90°quadrants from a random orientation and the nearest distance to each of the attributes was measured in each quadrant. We used randomly placed line-intercept transects (Marshall et al. 2000) for estimating volume of downed wood by piece size diameter classes (2 - 6, 7 - 29, 30 - 49, 50 – 74, ≥ 75; and ≥ 50, ≥ 30, ≥ 7 cm) and decay/hardness classes (> 50% decay, blocky or soil wood; ≤ 50% decay hard, intact; and fresh). At wren and random locations, we used two 12.5-m line-intercept transects placed at a 90° angle for minimum effort. But we used three 12.5-m line-intercept transects placed in a randomly oriented spoke with 60° angles at the 50 x 50-m survey grid points and at the nest sites, also using these measures to estimate availability of nest structures. We calculated density of tree stems and snags per ha by diameter (< 10, 10-29, 30-49, 50-74, ≥ 75; and ≥ 50, ≥ 30, ≥ 10 cm dbh), canopy, and decay and hardness (hard outside or soft outside) classes.

Statistical Analyses of Song Perch Locations

We used an unbalanced, completely randomized, split-plot, factorial analysis of variance (Steel et al. 1997) (ANOVA) to determine whether winter wrens in young and mature forests placed their territories closer to streams than would be at random and to assess habitat selection at their song perches. We set our significance level at $P \leq 0.05$. We grouped transects within the same general area (usually a watershed) into blocks, and these blocks were nested within seral stage (10 blocks in young forest, 9 blocks in mature forest). The ANOVA determined which habitat attributes (response variables) had significant between group differences for a) the two seral stages (young and mature) and b) the two types of locations (wren and random). Seral stage was the whole-plot factor and location was the split-plot factor. The experimental units for the whole-plot factor were the blocks nested within seral stage. We eliminated habitat attributes that were infrequent across locations and one attribute for pairs of attributes that were highly correlated ($r \geq 0.70$) and had a similar ecological interpretation. A rank transformation was used on all habitat attributes to normalize the residuals. However, estimated least-square means and standard errors were calculated using the unranked data.

We used a logistic regression model to determine a resource selection function that identifies those habitat attributes that best convey the probability of a wren location in these forest stands (Brennan et al. 1984, Manly et al. 1993). The resource selection function $w(x_1, x_2,\ldots,x_k)$ is directly proportional to the unknown resource selection probability function. It is estimated by modeling the conditional probability that an observation having a particular set of habitat attributes will be found at a wren location rather than at a random location, given that the observation is at one of the two locations (McCullagh and Nelder 1989, Manly et al. 1993). The habitat attributes used as covariates for the logistic regression model were those for which the ANOVA revealed significant differences in their amounts between wren and random locations. The logistic regression analysis proceeded in two steps. First, we used a mixed model logistic regression to determine whether seral stage had a significant effect on the conditional probability outlined above. The SAS macro GLIMMIX (Littell et al. 1996) was used to find

restricted (residual) pseudo likelihood (REPL) parameter estimates. The full model is:

$$\log\left(\frac{\tau_{ijk}}{1-\tau_{ijk}}\right) = \mu + s_i + a_{(i)j} + \beta_1 x_{1(ij)k} + \beta_2 x_{2(ij)k} + \ldots + \beta_p x_{p(ij)k} \quad [1]$$

where τ_{ijk} is the probability that an observation in a particular block and having a particular set of habitat attributes $\{x_1, x_2, \ldots, x_p\}$ will be found in the wren location rather than the random location, given that it is one of these locations; μ is the overall intercept; s_i is the effect of seral stage ($i = 1,2$); $a_{(i)j}$ is the random block effect $a_{(i)j} \sim N(0,\sigma_a^2)$ ($j = 1,2,\ldots,19$), which is nested within seral stage; $\beta_1, \beta_2, \ldots, \beta_p$ are the regression parameters, and the observations are indexed by $k = 1,2,\ldots,148$. Following the non-significant effect of seral stage along with negligible block-to-block variability, we streamlined the model and incorporated all random and wren locations in a simple logistic regression. Non-significant habitat attributes were also dropped producing a simplified model with only $q \leq p$ regression parameters, where all parameters are defined as in Equation 1:

$$\log\left(\frac{\tau_k}{1-\tau_k}\right) = \mu + \beta_1 x_{1k} + \beta_2 x_{2k} + \ldots + \beta_q x_{qk} \quad [2]$$

We will discuss [2] in the remainder of the paper, even though the actual resource selection function is of the form: $w(x_1, x_2, \ldots, x_k) = \beta_1 x_{1k} + \beta_2 x_{2k} + \ldots + \beta_q x_{qk}$.

Statistical Analyses of Nests and Nest Sites

We used log-likelihood Chi-square (G) tests and Bonferroni-adjusted Z-tests with 95% confidence intervals to test winter wren selectivity for nest substrates and nest substrate locations during 1995 and 1996 (Neu et al. 1974, Manly et al. 1993). We pooled nests from both breeding seasons because wrens reused nests between years. We pooled occupied and unoccupied nests because there were no identifiable criteria of unoccupied nests that distinguished them as dummy nests or as representing lower quality nest sites (Garson 1980, Wesolowski 1983). Males did not over-winter at the study area, therefore we reasoned the entire area was initially available each spring and we defined available habitat as the proportion of 50 x 50-m survey grid points (n = 365) within each category. If territoriality limits availability, we may have overestimated abundance of less common attributes including stream channel and bank, upturned root masses, and remnant old cut stumps. To determine whether males selected for type of nest substrate, we used the following categories based on our field observations: logs; snags including nests behind bark, nests in a crevice, or nests in a remnant old cut stump; upturned root masses; stream banks; and branches on trees or snags. For testing whether nest locations selected by males were independent of distance to stream, we used five distance categories from streams and noticeable seeps (0-5, 6-10, 11-50, 51-100, 101-300 m). The 0-5-m category includes the influence of riparian channels on vegetation extended up to 5 m on each side of streams. The 6-10-m category is transitional between riparian and upslope areas. The 51-100-m category is differentiated from the 11-50-m and 101-300-m categories because 51 m is greater than the mean distance to water in the stand (50-m) and winter wrens were commonly observed to fly between locations up to 100 m apart.

For determining habitats selected by males at nests, we used Multivariate Analysis of Variance (MANOVA) (SAS Institute Inc. 1988; Tabachnick and Fidell 1989). We compared nest sites with non-nest sites within territories, defining non-nest sites as the closest (≥ 25 m) 50 x 50-m survey grid point within the territory that lacked nests. We randomly selected one nest in territories with multiple nests. For the analyses, we also needed to separate into different strata those nest sites in the channel and along the immediate edges of streams 5-10 m-wide (5-10-m channel) from the other nests beyond the 5-10-m channel (other). This ensured that the non-nest sites paired with nest sites of these larger channels had the same general characteristic forest structure and topography for measuring habitat selection within the territory. Therefore, we paired nest sites and non-nest sites by territory, year, and location (5-10-m channel, n = 10; other, n = 37). Habitat attributes within these pairs were used as the multivariate response because of the dependence between nest and non-nest sites occurring within the same territory in the same year. For the MANOVA, we tested for differences in amounts of habitat attributes between 5-10-m channel and other nest sites, and for differences between nest and non-nest sites. If an interaction for a particular attribute occurred between 5-10-m channel and other nest sites, then we tested for differences between nest

and non-nest sites within each of these categories separately, corrected for experiment-wise error. Residuals were examined for homogeneity of variance and normality. We reduced the number of habitat variables analyzed by eliminating one attribute of a pair of attributes that were highly correlated ($r \geq 0.70$) and had similar ecological interpretations.

Results

Song Perches

We identified 77 wren locations in 1996. Forty winter wrens were located along 9.12 km of transect in young forest compared to 37 along 9.30 km in mature forest. Fourteen percent (11 / 77) of the wren locations were estimated as within 5 m of the actual location and hence, for these we could not identify type of song perch structures. For the remaining 66 song perches, winter wrens used downed wood (9), upturned root masses (9), snags (30), and trees (18). We measured 75 random locations in young (37) and mature (38) forest.

Few of the habitat variables we sampled showed that the structure of the forest differed significantly between the two seral stages. Generally, young stands compared to mature stands had more closely spaced understory snags and root masses, less coverage of < 0.5 m-high vegetation, and a more prominent deciduous overstory component (Table 1). In contrast, wren locations compared to random locations had overstory trees spaced farther apart and significantly less cover of vegetation < 0.5 m-high, including < 0.5 m-high shrub and moss (Table 1). From these findings, we infer that the lower strata likely had a combination of exposed mineral soil, rock, water, and downed wood. In both seral stages combined, we also observed that wren locations were significantly closer to streams than random locations although high variance was associated with this measure (Table 1). There was a significant interaction between seral stage and type of location for the total volume of downed wood ($P = 0.04$) suggesting its importance likely varied between seral stages. However, we did not detect any significant relationships between wren locations and volume of down wood for any piece size diameter class.

For the full mixed model logistic regression (Equation 1), we used mean distance to overstory tree (Over), cover of moss (Moss), cover of vegetation < 0.5 m-high (Veg), and distance to stream (Str). We eliminated shrub < 0.5 m-high because it is a component of vegetation < 0.5 m-high (Table 1). Seral stage did not have a significant effect in the model and it was eliminated from further analyses (Table 2). In the full model, both mean distance to overstory tree and cover of moss were significant at predicting the conditional probability that winter wrens would use a location in either seral stage (Table 2). The simple logistic regression best-fit model (Equation 2) also identified

TABLE 1. Results from split-plot ANOVA for differences between young (n = 77) and mature (n = 75) seral stages (main effect; df 1, 17), and between wren (n = 77) and random (n = 75) locations (split-plot effect; df 1, 17) using rank transformed habitat attributes for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

	Seral stage				Location type			
	Mean (SE)		Main effect		Mean (SE)		Split-plot effect	
Habitat attribute	Young	Mature	F	*P*	Random	Wren	F	*P*
Distance to stream (m)	242 (87)	49 (91)	0.66	0.42	150 (64)	142 (64)	10.44	0.01
Mean distance to overstory tree (m)	3.6 (0.4)	4.8 (0.4)	3.82	0.06	3.9 (0.3)	4.5 (0.3)	11.77	<0.01
Mean distance to understory snag (m)	5.3 (0.8)	8.3 (0.8)	6.46	0.02	6.5 (0.6)	7.0 (0.6)	3.27	0.09
Distance to root mass (m)[1]	9.7 (1.4)	18.2 (1.4)	9.37	0.01	15.2 (1.4)	12.7 (1.4)	1.68	0.21
Deciduous overstory canopy cover (%)	21.8 (4.0)	3.3 (4.3)	25.77	<0.01	11.6 (3.4)	13.5 (3.4)	3.15	0.10
Vegetation cover < 0.5 m-high (%)	3.1 (0.9)	5.7 (0.9)	6.43	0.02	5.3 (0.8)	3.5 (0.8)	6.34	0.02
Shrub < 0.5 m-high cover (%)	3.1 (0.9)	5.0 (1.0)	3.86	0.07	4.8 (0.9)	3.2 (0.9)	4.29	0.05
Moss cover (%)[1]	24.9 (7.0)	41.7 (7.4)	1.02	0.33	38.1 (5.4)	27.9 (5.5)	7.77	0.01

[1]Sample size adjusted for 1 (distance to root mass) and 3 (moss cover) missing data points.

TABLE 2. Parameter estimates for the full model (Equation 1). Block-to-block variability is treated as a random factor. The intercept represents the mature seral stage and S represents the additional effect of the young seral stage over-and-above the mature seral stage. The estimate of the variance component is $\hat{\sigma}_a^2 \cong 0.000$.

Parameter[1]	Estimate	*P*
Intercept	-1.0851	0.12
Seral Stage	0.2679	0.54
Over	0.3706	0.01
Moss	-0.0100	0.05
Str	0.0001	0.86
Veg	-0.0400	0.26

[1]Over = mean distance to overstory tree, Moss = cover of moss, Veg = cover of vegetation <0.5 m-high, and Str = distance to stream.

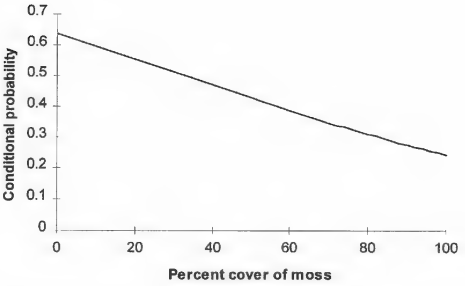

Figure 2. Predicted conditional probability (Equation 2) of a winter wren occupying a location: $\tau_k = e^{-0.784+0.319\cdot\overline{over}-0.017\cdot moss_k} / (1+e^{-0.784+0.319\cdot\overline{over}-0.017\cdot moss_k})$ as cover of moss ($moss_k$) changes from 0 to 100% while mean distance to overstory tree ($\overline{over}$) is held at its estimated mean (4.2 m).

mean distance to overstory tree and cover of moss as the best predictors of male winter wrens using a location (Figures 1 and 2). The high Reduction of Deviance ($-2[\text{LogL}(\mu)-\text{LogL}(\mu, \beta_1, \beta_2)] = 13.958$, $P = 0.0009$) reflects the collective significance of these two factors. Both distance to stream and cover of vegetation < 0.5 m-high did not contribute significantly to the model. The non-significant Hosmer and Lemeshow Goodness of Fit statistic indicates closeness between predicted and observed probabilities, and suggests the model is a good fit. The logistic regression model shows that the greater the mean distance to overstory tree the higher the probability that winter wrens will use a location, with a maximum at ~15 m

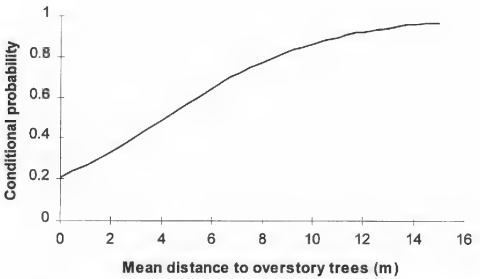

Figure 1. Predicted conditional probability (Equation 2) of a winter wren occupying a location: $\tau_k = e^{-0.784+0.319\cdot over_k-0.017\cdot\overline{moss}} / (1+e^{-0.784+0.319\cdot over_k-0.017\cdot\overline{moss}})$ as mean distance to nearest overstory tree ($over_k$) changes from 0 to 15 m while moss coverage ($\overline{moss}$) is held at its estimated mean (32%).

(Figure 1). The negative relationship between wren locations and cover of moss has a smaller range of probability estimates for predicting a winter wren location (Figure 2). Wrens are more likely to occur in sites without moss.

Nests and Nest Sites

We found 99 nests during 1995 and 1996 of which 95 were associated with territories. Territories ranged in size from 0.37 to 2.38 ha. Some territories had multiple nests (22% in 1995 and 53% in 1996), some territories had single nests (35% in 1995, 47% in 1996) and in other territories, we were unable to find any nests (43% in 1995). Nests occurred at a range of heights in the understory of the forest (35 cm to 285 cm; mean heights 70 cm in stream banks to 190 cm on branches). Male winter wrens showed selectivity for type of nest substrate ($G = 124.9$, $P < 0.01$). Upturned root masses and stream banks were used more than expected, logs and snags (bark, crevice, and stump) were all used in proportion to their availability, but branch substrates were used less than expected (Figure 3).

Males showed selectivity for streams ≤ 10 m-wide when building their nests ($G = 30.2$, $P < 0.01$; Figure 4), although streams < 5 m-wide tended to become dry by late May to early June. All nests in stream banks (12) and in upturned root masses (20) were ≤ 5 m from streams. Nests in other substrates occurred over a range of distances, but 52% were also ≤ 5 m from a stream (15 of 38 log nests, 16 of 23 snag nests including

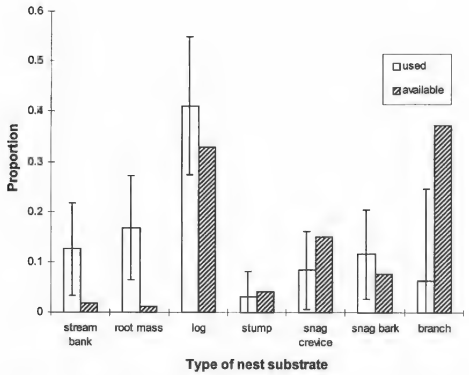

Figure 3. Proportions of substrates in which male winter wrens built nests compared to proportions of substrates available in the Roberts Creek Study Forest with 95% confidence intervals (Bonferroni-adjusted Z-tests, K = 7).

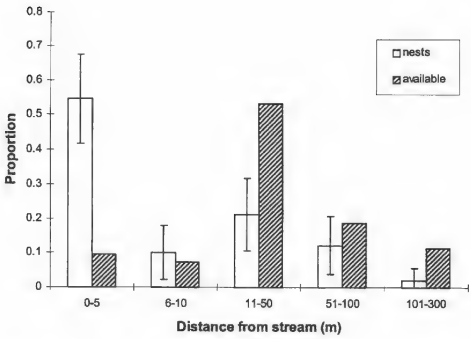

Figure 4. Proportions of winter wren nests and availability of habitat at different distances from streams in the Roberts Creek Study Forest with 95% confidence intervals (Bonferroni - adjusted Z-tests, K = 5).

stumps, and 4 of 6 branch nests). Nests occurred in proportion to habitat availability in the 6-10-m and 51-100-m distance categories from streams. Fewer nests than expected were located in the 11-50-m category. Although some nests were > 100 m from a stream, few winter wrens tended to use these locations.

Some habitat attributes differed between nest and non-nest sites, but these differences were not consistent for the 5-10-m channel nest sites and the other nest sites beyond the 5-10-m channels (Table 3). Compared to non-nest sites, nest sites beyond the 5-10-m channels had significantly fewer live stems (≥ 50, 30-49, and ≥ 10 cm dbh classes), live stems and snags combined (30-49 cm dbh

TABLE 3. Mean habitat attributes at nest sites and paired non-nest sites (multivariate response) by habitat type (channel, i.e., 5-10-m and other, i.e., away from 5-10-m channels). Significant ($P \leq 0.05$) values from the MANOVA are presented separately by habitat type if an interaction was detected or pooled over habitat types if no interaction was detected.

		Nest site		Non-nest site		MANOVA		
Habitat attribute	Habitat type	Mean	SE	Mean	SE	df (n, d)	F	*P*
Downed wood 30 - 49 cm (m^3/ha)	Channel	140.6	28.4	77.6	18.8	1,9	4.45	0.06
	Other	94.7	13.0	127.1	11.9	1,36	4.50	0.04
Live stems 30 - 49 cm dbh (stems/ha)	Channel	115	20	85	22	1,9	0.89	0.37
	Other	99	11	232	27	1,36	24.96	<0.01
Live stems and snags 30 - 49 cm dbh (stems/ha)	Channel	145	25	110	27	1,9	1.15	0.31
	Other	137	14	257	27	1,36	27.63	<0.01
Live stems ≥ 50 cm dbh (stems/ha)	Channel	95	23	85	22	1,9	0.13	0.73
	Other	107	12	184	22	1,36	12.49	<0.01
Live stems ≥ 10 cm dbh (stems/ha)	Channel	400	47	325	62	1,9	0.871	0.36
	Other	481	40	727	40	1,36	27.91	<0.01
Live stems < 10 cm dbh (stems/ha)	Pooled	313	33	923	203	1,46	8.62	0.01
Live stems and snags < 10 cm dbh (stems/ha)	Pooled	505	51	1127	204	1,46	8.40	0.01
Live stems and snags ≥ 75 cm dbh (stems/ha)	Pooled	31	5	72	17	1,46	6.04	0.02
Live stems and snags ≥ 50 cm dbh (stems/ha)	Pooled	137	11	204	20	1,46	12.35	<0.01
Distance to upturned root mass (m)	Pooled	9.0	1.4	12.8	1.3	1,45	3.93	0.05
Deciduous shrub cover (%)	Pooled	5.4	1.0	3.4	0.6	1,46	5.02	0.03
Ground cover (%)	Pooled	82.0	2.2	88.5	1.0	1,46	7.55	0.01

class), and volumes of medium sized downed wood in the 30-49 cm diameter piece size class. Yet these densities of live stems and snags at the nest sites beyond 5-10-m channels were similar to those measured at both nest and non-nest sites in 5-10-m channel areas (Table 3). Seven additional habitat attributes also indicated differences between nest and non-nest sites using the pooled nest sites (Table 3). Nest sites compared to non-nest sites had fewer live stems (< 10 cm dbh class), live stems and snags combined (≥ 75, ≥ 50, < 10 cm dbh classes), and less exposed ground of duff and rock. Cover of deciduous shrubs was greater and root masses were closer to the nest substrate.

Discussion

Habitat Values of Small Streams

In both young and mature stands, the locations of song perches, thus territories of winter wrens were associated with streams (Table 1). Furthermore, the overall lack of interactions between seral stage and type of location indicated that winter wrens, independent of stand age and stage of seral development, selected a suite of habitat attributes to provide optimal habitat (Table 1). Winter wrens did not appear to use habitat differently as the forest developed from young to mature, and this finding further supports that age alone can be a poor criterion for managing habitats for wildlife (Rotenberry and Wiens 1980, Hayes et al. 1997, Waldien et al. 2000). Instead, occurrence and distribution of structural attributes and small streams with their unique characteristics, such as channel morphology (stream banks), influenced the spatial distribution of winter wrens in both seral stages of coastal temperate forests.

The heterogeneous forest structure associated with streams was important for providing winter wrens with nesting opportunities. Nests were located closer to streams relative to their availability (Figure 4) and wrens chose types of nest substrates (Figure 3) associated with small streams. Yet, wrens selected similar nest sites whether adjacent to streams 5-10 m-wide that had structurally distinct riparian areas including banks, overstory gap and vegetation or whether in other areas away from these 5-10-m channels (Table 3). However, fewer differences were apparent between the forest structure of nest and non-nest sites near streams 5-10 m-wide, than elsewhere (Table 3). A male may build several nests in his territory, but fewer nests may be built in less favorable habitat (Armstrong 1956, Armstrong and Whitehouse 1977). Thus, when establishing their territories males may select for streams to obtain more nesting opportunities. In turn, the structure contributed by vegetation and terrain characteristics of streams 5-10 m-wide may offer more potential opportunities for wrens than do streams < 5 m-wide (Table 3). Other than nesting opportunities, factors that likely contribute to habitat selection of winter wrens are higher forage quality (Armstrong 1956, McLachlin 1983, Holmes and Robinson 1988, Van Horne and Bader 1990) and thermoregulation (Armstrong and Whitehouse 1977), and we hypothesize that riparian habitats may positively influence these factors (Waterhouse 1998).

Gaps in Upslope Habitats

Although winter wrens selected for song perches and nests nearer to streams when available, they also used habitats upslope of streams (Table 1, Figure 4). For example, stream location was not selected as a significant predictor of song perch location in the logistic regressions (Table 2). Thus, winter wrens use a range of habitat conditions for nesting and singing. The similarity between nest and song perch microhabitat patches is expected because males often use the nest substrate as a song perch when they are advertising the nest (Garson 1980).

Nests within territories, and song perches within the surrounding young and mature forest were at relatively open sites in the forest understory (Tables 1, 3). Our logistic regression model suggests winter wrens are more likely to sing in open sites because it was more probable that wrens would occur in locations with a 10-15 m mean distance to an overstory tree. In either the young or mature forest, this mean distance suggests a gap in the overstory canopy. However, our percent estimates of overstory canopy cover were not significantly lower at wren locations or nest sites compared to the surrounding forest. Therefore understory conditions associated with gaps may be more important for winter wrens because lateral branch growth diminishes the size of the overstory gap. The lack of moss cover and the significant association of upturned root masses with wren locations and nest sites confirm that wrens select disturbed sites.

Disturbed sites had stream banks or residual developmental gapmakers including snags, root masses, and downed wood available for nest substrates (Figure 4). During the breeding season in 1996, we observed that water collected in pits from uprooted trees turning these disturbed sites into locally wet sites. This process creates distinct microclimates (Beatty and Stone 1986, Schaetzl et al. 1989) and likely provides fine-scaled sites for foraging and nesting. The winter wren in other regions is associated with areas of localized disturbance that have canopy openings, downed wood, upturned roots, and with dense understory vegetation (Wesolowski 1983, Holmes and Robinson 1988, Carey et al. 1991, Tobalske et al. 1991). Thus, nest substrates and nest sites selected by winter wrens are often created through processes of succession and natural disturbance (Spies et al. 1990, Lertzman et al. 1996) and are linked directly to gaps. The structure and microclimate of developmental gaps provide alternate nesting and foraging habitats in upslope areas and further enhance the value of streamside habitats for winter wrens.

Although our research is limited to the winter wren, it is likely that other wildlife in the drier Coastal Western Hemlock Dry Maritime Subzone (CWHdm) benefit from the distinct habitat qualities of small streams including channel morphology, forest structure and microclimate that are associated with winter wrens. Reserve areas or aggregates of forest structure retained adjacent to small streams or seeps can be used to manage for streamside habitats. Some management options available in British Columbia for retaining forest structure and associated wildlife habitat within stands include retention of small patches of trees (wildlife tree patches) and riparian management areas that are established adjacent to streams (B.C. Ministry of Forests and B.C. Ministry of Environment 1995, 1999). The area within 5 m of small stream banks was most important for nest sites of winter wrens, however, they also use areas beyond this narrow band next to stream banks. Hagar (1999) reported for the central Oregon Coast Range, that along first- to third-order streams, winter wrens in mature Douglas-fir/western hemlock riparian forest buffers >30 m wide approached minimum abundances comparable to those in unlogged forest.

Our research also exposes the value of canopy gaps and gapmakers as habitat sources in both riparian and upslope areas. Alternative silviculture systems can be used to retain or recruit structural features that mimic gapmakers (e.g., snags, logs, and uprooted trees). Removing small groups of trees (group selection) is one alternative for mimicking canopy gaps (Lertzman et al. 1996, Franklin et al. 1997). But prescriptions mimicking canopy gaps need to consider retention of structural features within the harvested area to also mimic the gapmakers. This retention is particularly important when group selection is cycled throughout the entire forest matrix and when the desired structural features have developmental periods longer than the rotation or are required in large numbers for biodiversity objectives (Franklin et al. 1997).

Acknowledgements

This study received financial support from the British Columbia Ministry of Forests and the Canada-British Columbia Forest Resource Development Agreement: FRDA II. Staff of the Sunshine Coast Forest District and the Vancouver Forest Region provided logistic support. We thank Kevin MacPherson, Kate Hagmeier, Duane Sept, Rebecca Boettger, and Karen Leonard for field assistance, and Brenda Dale for external review.

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Received 9 November 2001
Accepted for publication 10 July 2002

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Craig A. Steele,[1] **Edmund D. Brodie, Jr.,** Department of Biology, Utah State University, 5305 Old Main Hill, Logan, Utah 84322

and

James G. MacCracken, Timber Department, 300 Fibre Way, Longview Fibre Company, Longview, Washington 98632

Influence of Forest Age on Densities of Cope's and Pacific Giant Salamanders

Abstract

We surveyed first-order streams in forest stands 0–94 yr old on industrial timberlands in the Cascade Mountains of southern Washington during the summer of 1998 and 1999 to determine how short-term changes in forest age can affect the abundance of the stream-breeding Cope's and Pacific giant salamanders. Based on results from cross-validated regression trees, densities of both species were unrelated to changes in forest age or any other habitat variable measured. There was also no difference in any of the measured habitat variables between streams in which a species was present and streams in which it was not detected. However, densities of the Pacific giant salamander were negatively correlated to percent of riparian canopy cover in one of the years.

Introduction

The stream-breeding giant salamanders (*Dicamptodon* spp.) have received much attention with respect to their habitat associations (Hawkins et al. 1983, Corn and Bury 1989, Parker 1991, Wilkins and Peterson 2000). Several studies correlated the presence of giant salamanders with stream habitat characteristics such as high gradient riffles (Hawkins et al. 1983, Corn and Bury 1989) and coarse substrates (Parker 1991, Wilkins and Peterson 2000) or have shown increases of giant salamanders in streams running through recently clearcut timber stands (Murphy et al. 1981, Murphy and Hall 1981, Hawkins et al. 1983). Other studies have concluded that giant salamanders are most often found in or near streams surrounded by older forest stands (Corn and Bury 1989) or in stands that have old growth characteristics such as large conifers (Gomez and Anthony 1996). This knowledge of old growth association is valuable, however, little old growth exists today in National Forests or on private timberlands. Because the current ranges of these amphibians occur partly on industrial timberlands it is also important to study habitat associations and population distribution of these animals in forests that rarely reach old growth status and are subject to regular, intensive harvest management.

Many previous studies did not differentiate between Cope's giant salamander (*D. copei*) and Pacific giant salamander (*D. tenebrosus*) when examining how this genus responds to changes in forest age or other habitat variables. It is often difficult to differentiate between Cope's giant salamander and larval Pacific giant salamanders in the field, and there is generally an unstated assumption that, despite differences in morphology and life history, the two species respond similarly to changes in environmental parameters. Cope's giant salamander was not distinguished from larval Pacific giant salamanders until its description in 1970 (Nussbaum 1970). Cope's giant salamander is an obligate neonate, remaining in an aquatic larval stage throughout its life. Metamorphosed individuals are found rarely, whereas neotony is only occasionally exhibited in some populations of the Pacific giant salamander. The difficulty of distinguishing between neotenic Cope's giant salamanders and sympatric larval Pacific giant salamanders in the field is likely preventing comparative field studies on these two species. Morphological differences between the species are slight, making field identification difficult. It has been assumed that the two species respond similarly to changes in stream substrate (Wilkins and Peterson 2000), but it has not been determined how Cope's giant salamander responds to changes in forest age and whether their responses are similar to those of Pacific giant salamanders.

[1]Author to whom correspondence should be addressed. Current address: School of Biological Sciences, Washington State University, Pullman, WA 99164-4236. E-mail: steele@mail.wsu.edu

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This study, performed in areas of regenerating second-growth forests, intended to examine how the abundance of Cope's giant salamander and sympatric larval Pacific giant salamanders are associated with changes in forest age. This study also intended to examine stream habitat associations of each species.

Methods

The study took place on corporate timberlands in southern Skamania County, Washington, between 45°46' to 45°38'N latitude and 122°14' to 121°53'W longitude (Figure 1). Annual precipitation occurs mostly as rains from October through March and ranges from 229 to 305 cm (Daly et al. 1994). Geology of the area is mostly basalt and andesite flows with their associated breccias and tuffs (Franklin and Dyrness 1988). Elevations range from 240 to 800 m. The region experienced nine localized stand-replacing fires between 1902 and 1952 (Felt 1977). The area is managed primarily for the production of wood pulp and small sawlogs with even-aged silviculture and 50-70 yr rotations. Dominant vegetation varies with harvest management, but Douglas-fir (*Pseudotsuga menziesii*) is usually the dominant conifer as it is commonly planted after timber harvest. Noble fir (*Abies procera*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and red alder (*Alnus rubra*) also contribute to the overstory at most sites. The understory comprises huckleberries (*Vaccinium* spp.), devil's club (*Oplopanax horridum*), blackberries (*Rubus* spp.), salal (*Gaultheria shallon*), and western sword fern (*Polystichum munitum*).

We located all first-order streams, using maps of the study area, across the range of forest ages available. Ages of surrounding timber stands were calculated from the time of replanting. Stands < 70 yr had been clearcut up to the stream banks and replanted with Douglas-fir seedlings. Stands > 70 yr were rare and likely regenerated naturally after one of the regional fires. While timber harvest was not the primary disturbance for streams in these oldest stands, two streams were sampled to provide additional data from older aged forests that are uncommon on industrial timberlands.

Streams with continuous permanent flow were located in the field to confirm their presence and to determine if they met the selection criteria for sampling. Streams selected for sampling measured ≤2 m wide, had a maximum depth of ≤15 cm, and

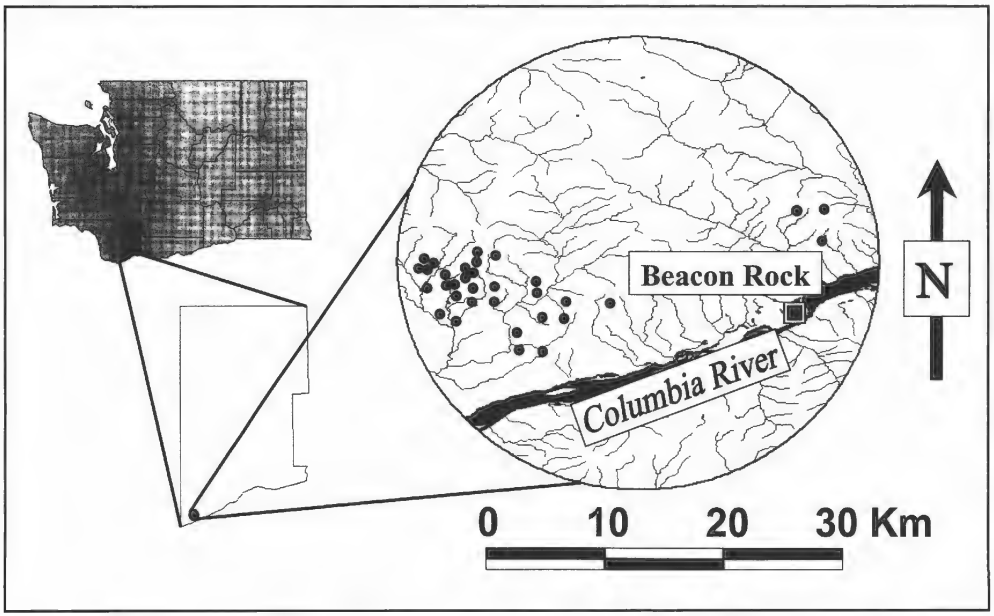

Figure 1. Location of streams sampled in Skamania County, Washington.

had an unembedded substrate that was visually estimated to comprise more than half cobble and gravel. These criteria ensured that appropriate stream habitat for giant salamanders (i.e., unsilted rocky substrates) was sampled in streams of a manageable size while minimizing variation of physical stream characteristics. Because of the high gradient and small size of these headwater streams, sampling was precluded in slow-water habitats such as pools, runs, or glides. All streams meeting these criteria in the study area were sampled. Twenty-nine streams that met the selection criteria were surveyed in 1998. In 1999 these same streams were resampled along with an additional four streams. All streams were within 29 km of each other.

Three plots in each stream were sampled between June and August during 1998 and 1999. Selection of plots within a stream began 10 m below the immediate headwaters (i.e., where the headwaters first formed a recognizable channel). Plots were 2 m long, as wide as the wetted width, and separated from each other by at least 10 m. All plots were located upstream from roads. We measured these stream and riparian habitat characteristics at each plot before sampling for salamanders began: water temperature, stream depth, width, gradient, aspect, elevation, and percent cover of trees and tall shrubs. A single measurement of stream depth for each plot was obtained by averaging nine depth measurements to the nearest centimeter: depth of the thalweg (deepest channel of the stream) at the middle, upstream, and downstream edges of the plot, and depths at midpoints between each thalweg measurement and either bank. Stream width was averaged to the nearest 10 cm from measurements at the middle, upstream, and downstream edges of the plot. Upstream gradient of the stream was measured with a clinometer. Elevation and aspect were taken from topographic maps. Percent canopy closure was measured with a spherical densiometer at the middle of each plot. The timber stands surrounding the streams were relatively homogenous, even-aged stands. Measurements of habitat variables were averaged from the three plots to give an overall measurement of the stand and stream characteristics for individual streams.

Sampling for salamanders began at the upstream portion of each plot and moved downstream to a net placed across the stream at the lower end of the plot. Salamanders were collected by systematically placing a square framed dip net in the plot, removing all cover items, raking the substrate for approximately 0.5 m in front of the dip net, and repeating the process with the intention that all salamanders would either be caught by hand or swept into the dip net. Periodically during the sample, the large net spanning the stream was searched for salamanders. Because large larvae will leave a stream during intensive sampling, a 1-m wide plot on the stream bank on either side of the stream was also intensively searched for amphibians that had either left the stream during sampling or were associated with stream edges. This 1-m wide terrestrial plot was subjected to a systematical search in which all cover items were turned over and the substrate was raked. Cover items were replaced in all plots at the end of the search.

Because larvae are often difficult to identify to species in the field, it was necessary to preserve all captured larvae in formalin for later identification in the laboratory. Using criteria established by Nussbaum (1970, 1976), preserved larvae were identified as either Cope's or Pacific giant salamander. The Pacific giant salamander usually has 6-7 gill rakers on the first and second gill arches while Cope's giant salamander has 4-5. Also, the Pacific giant salamander usually has 5-6 rakers on the fifth and sixth gill arches while Cope's giant has 3-4 (Nussbaum 1976). Gill rakers were counted for each specimen to determine the species.

Salamander abundance and habitat data of each stream were averaged from the three plots to give an overall measurement of stream habitat characteristics and salamander abundance for an individual stream in each year. Data from each year were analyzed separately using regression tree analysis with the computer program S-Plus 2000 for Windows (S-Plus 1999). Regression trees are used to uncover structure or patterns in data when either a set or a single predictor variable is used to estimate a single response variable (Clark and Pregibon 1992) and are appropriate when classification of data based on threshold values is needed rather than a linear association (Verbyla 1987). Regression trees are advantageous because data may be assumed to be non-normally distributed, both continuous and categorical data may be used, and data also do not need to be linearly related to predictor variables. We performed regression tree analysis to examine the

mean number of salamanders caught per stream relative to forest age. Optimally sized regression trees were selected based on the results of a cross-validation process (Breiman et al. 1984) repeated 500 times. The presence or absence of either species in a stream was determined from both years of sampling. Comparative, two-tailed Student's t-tests, or Welch's t-test in the case of unequal variance between groups, were used to test for differences in habitat variables between streams in which the species was present and streams in which it was not detected. The 5% significance level of the *P*-values for these tests were adjusted using the Bonferroni correction method described by Rice (1989).

Results

In 1998 a total of 166 larval Cope's and 98 larval Pacific giant salamanders were captured from the 29 streams sampled. When present, the range of densities of Cope's and Pacific giant salamanders were 0.05–1.16/m^2, and 0.05–0.79/m^2. Of the 29 streams sampled, Cope's giant salamanders were in 23 (79%) and Pacific giant salamanders were in 16 (55%). Twelve streams contained both species; the ratio of Cope's to Pacific giant salamanders in these streams was 1.0:1.2. In 1999, 105 larval Cope's and 114 larval Pacific giant salamanders were captured from the 33 streams sampled. When present, ranges of densities for Cope's and Pacific giant salamanders were 0.06–1.43/m^2 and 0.06–2.5/m^2. Of these streams sampled, Cope's giant salamanders were detected in 19 (58%) and Pacific giant salamanders in 16 (48%). Both species of giant salamanders were detected in 10 of the streams; the ratio of Cope's giant salamanders to Pacific giant salamanders in these streams was 1.0:1.1.

Densities between years were significantly correlated for both Cope's ($r = 0.65$, $P < 0.01$) and Pacific giant salamanders ($r = 0.44$, $P = 0.02$). Regression trees based on the capture data for either year (Figure 2) were not supported through cross-validation and are not presented. Of the 33 streams sampled over the 2-yr period, none of the measured habitat variables was significantly different between streams in which either species was present and streams in which they were not detected (Table 1).

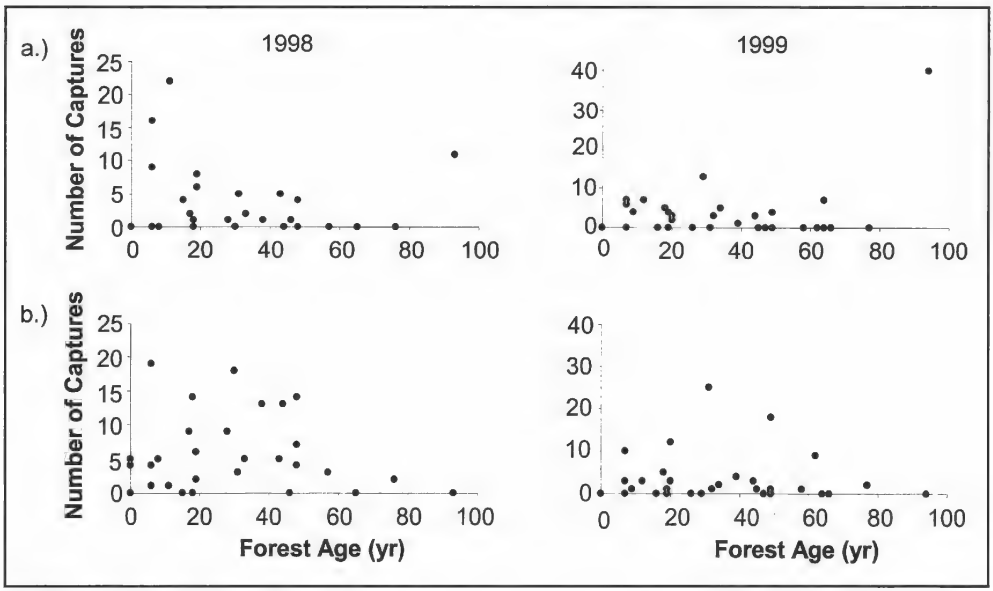

Figure 2. Scatterplots showing change in density of Pacific giant salamanders (a.) and Cope's giant salamanders (b.) in 1998 and 1999. Some data are obscured by overlapping points.

TABLE 1. Comparison of mean (SE) measured variables between streams in which a species was detected and streams in which it was undetected. [w] indicates that Welch's t-test of unequal variances was performed.

Variable	Detected	Undetected	*P*
Cope's giant salamander			
Number of streams	24	9	
Canopy cover (%)	79.4 (5.3)	85.1 (4.6)	0.43[w]
Gradient (degrees)	16.5 (1.2)	17.3 (2.2)	0.77
Average width (cm)	82.8 (3.5)	75.0 (4.5)	0.23
Average depth (cm)	4.3 (0.4)	3.9 (0.5)	0.61
Forest age (yr)	29.4 (4.3)	43.7 (10.2)	0.14
Water temperature (C)	9.4 (0.3)	9.8 (1.1)	0.72[w]
Elevation (m)	552.2 (32.4)	504.0 (59.1)	0.46
Pacific giant salamander			
Number of streams	18	15	
Canopy cover (%)	76.4 (6.9)	86.5 (2.6)	0.19[w]
Gradient (degrees)	15.3 (1.4)	18.5 (1.5)	0.14
Average width (cm)	85.9 (4.2)	74.5 (3.3)	0.05
Average depth (cm)	4.6 (0.5)	3.7 (0.2)	0.11[w]
Forest age (yr)	30.6 (5.3)	36.6 (6.9)	0.5
Water temperature (C)	10.3 (0.5)	8.5 (0.4)	0.01[w]
Elevation (m)	550.0 (34.6)	525.5 (47.5)	0.67

Discussion

The inability to cross-validate any of the regression trees suggests that either none of the habitat variables we measured was an effective predictor of salamander density or that the high levels of variance in the data prevented a consistent response pattern from being determined. However, an examination of the data shows that high densities of Pacific giant salamanders during 1998 were seen in streams located in recently clearcut forests (Figure 2). Elevated densities of Pacific giant salamanders are often observed in streams running through recently harvested timber (Murphy et al. 1981, Murphy and Hall 1981, Hawkins et al. 1983) and are considered to reflect the removal of riparian canopy cover, which temporarily increases aquatic production and produces an abundance of invertebrate prey. As in these previous studies, densities of Pacific giant salamanders in 1998 are negatively correlated with canopy cover ($r = 0.65$, $P < 0.001$). Patterns of density of Cope's giant salamanders differed from those of Pacific giant salamanders and were not correlated with canopy cover. Because of the high degree of variation in the number of captures between years for both species, it remains unclear if densities of Cope's giant salamander respond to changes in habitat parameters in the same way that has been documented for Pacific giant salamanders by other authors. A concerted effort by researchers to become familiar with differentiating Cope's and Pacific giant salamanders will be necessary to further our understanding of the ecological differences between these species.

Acknowledgements

This paper benefited from comments made by Dr. Joseph Beatty and one anonymous reviewer. Research was made possible by the Washington Department of Fish and Wildlife permit #98-173-C and was funded by Longview Fibre Company. Specimens were deposited in the Collection of Vertebrates, Department of Biology, University of Texas at Arlington.

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Received 26 December 2001
Accepted for publication 10 June 2002

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Northwest Science Notes

The purpose of Notes is to publish papers typically less than five pages in length. No specific format or content is required for notes published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

Brian W. Moser[1], Potlatch Corporation, Hybrid Poplar Program, Boardman, Oregon 97818-0038

Reproductive Success of Northern Saw-whet Owls Nesting in Hybrid Poplar Plantations

Abstract

I studied northern saw-whet owl nest productivity and survival in hybrid poplar plantations in eastern Oregon. I placed twenty-five nest boxes in 2- to 5-yr-old plantations and monitored them during the 1999 nesting season. Nine nesting attempts were made and eight were successful. Daily survival rates for eggs and nestlings as estimated by the Mayfield method were 0.9919 ± 0.0025. Clutch size, number of eggs hatched, and number of fledglings for all nesting attempts were 5.22 ± 0.49, 4.33 ± 0.69, and 3.55 ± 0.60. Hybrid poplar plantations can provide suitable nesting habitat for northern saw-whet owls if nest boxes are provided.

Introduction

The establishment of large, hybrid poplar (*Populus* spp.) plantations in North America is becoming increasingly common with the forest products industry because these fast-growing trees produce abundant wood fiber in a short period of time. In the past 15 yr, over 28,000 ha of hybrid poplar plantations have been established in the Pacific Northwest to produce fiber for both paper and dimensional lumber products (Heilman et al. 1995, Stanton et al. 2002).

Little is known about the influence of these plantations on bird communities. Published studies of bird use of hybrid poplar plantations are few and relatively recent, and focused primarily in the Midwest (Christian et al. 1997, Hanowski et al. 1997). Furthermore, these studies document wildlife use of plantations, rather than reproductive success. Because density alone can be a misleading indicator of habitat quality (Van Horne 1983), it is also important to measure reproductive success in these plantations.

[1]Current Address: Potlatch Corporation, P.O. Box 1388, Lewiston, Idaho 83501-1388.
E-mail Brian.Moser@potlatchcorp.com

Northern saw-whet owls (*Aegolius acadicus*) are secondary cavity nesters that use both natural and artificial cavities in forested habitats throughout North America (Cannings 1993). Reproductive success of northern saw-whet owls appears to vary geographically. Marks and Doremus (2000) studied northern saw-whet use of nest boxes in southwestern Idaho and documented mean annual occupancy rates of less than 5%. Mean number of fledglings was 3.3 per nesting attempt and 4.8 per successful nest. Cannings (1993) reported average clutches in British Columbia of 5.67 eggs and mean fledging rates of 2.68 young per nesting attempt and 3.47 young per successful nest. Murray (1976) reported mean clutch size of 3.79 eggs along the Pacific coast and 4.96 eggs in eastern North America. None of these studies estimated daily survival rates of eggs or young. The objectives of this study were to: 1) document the reproductive success of northern saw-whet owls nesting in hybrid poplar plantations in eastern Oregon, and 2) compute daily survival rates of eggs and young.

Study Area

The study was conducted on a 7050 ha complex of hybrid poplar plantations in the Columbia River

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Basin, Morrow County, Oregon. The natural vegetation in this region is steppe and shrub-steppe (Franklin and Dyrness 1988), and soil types are sandy and sandy loam. Topography varies from flat to slightly undulating with elevations ranging from 150 to 250 m. Annual precipitation averages 22 cm (Ruffner 1978), most of which falls in late winter and early spring. Drip-irrigated plantations were first established in 1994, primarily on former agricultural croplands irrigated by center-pivot systems. Tree height and diameter growth average 3 m and 2.5 cm per yr. Plantations are managed on a 7- to 10-yr rotation, therefore few trees become large enough to provide natural cavities for nests.

Methods

I placed 25 nest boxes 3-5 m high on trees in four plantation age classes (2- to 5-yr-old) during fall 1998. I checked nest boxes for occupancy beginning 7 April 1999, and continued to monitor occupied nest boxes every 3-4 days from incubation to fledging to document the fate of each nest. Nests were considered successful if at least one young fledged. I estimated daily survival rates of eggs and nestlings for each nest using the Mayfield method (Mayfield 1961, 1975). Estimates were calculated using the program MAYFIELD (Hines 1996), which was developed based on Bart and Robson (1982). I assumed constant survival over the entire nesting period. When an egg failed to hatch, I assumed mortality of the embryo at the approximate midpoint between the hatching date of the first egg and the last egg in that nest. Values reported are mean ± SE.

Results

Of nine nesting attempts, eight were successful for a total nest box occupancy rate of 36%. I found at least one successful nest in each of the four plantation age classes. I discovered all eight successful nests during the incubation period. Furthermore, I determined that the failed nest had been deserted by the time I found it because the partial clutch of two eggs was cold and no adults were observed near the nest. Thus, I could not compute daily survival estimates for this nest. Daily survival rate for the eight successful nests was 0.9919 ± 0.0025. Clutch size for all nine nests was 5.22 ± 0.49. Of these clutches, 4.33 ± 0.69 eggs hatched. Number of fledglings for all nine nests was 3.55 ± 0.60. The only causes of mortality for eggs were either infertile eggs or death of embryos. None was lost to predators. I was unable to determine the cause of nestling mortality because siblings quickly consumed nestling carcasses, leaving only the bones in the nest.

Discussion

Daily survival rates during the entire nesting period were relatively high, probably due to lack of typical arboreal mammalian nest predators, such as squirrels, in these plantations (Moser et al. 2002). Eggs failed to hatch due to either infertility or death of the embryo from unknown causes as suggested by Cannings (1993), because no other causes of mortality were apparent. Although I could not determine the cause of nestling mortality, Cannings (1993) suggested that most nestling deaths were likely due to starvation. However, Houston et al. (1998) reported rare instances of siblicide in great horned owls (*Bubo virginianus*). No published data exist on siblicide in northern saw-whet owls.

Nest box occupancy rates appeared to be higher in this study than those reported by Marks and Doremus (2000) for northern saw-whet owls nesting along the Snake River in Idaho. Mean clutch size from this study was comparable to that reported by Cannings (1993) for North America, and exceeded those values reported by Murray (1976) for both eastern and western North America. Mean number of fledglings from this study exceeded those reported by both Cannings (1993) and Marks and Doremus (2000). These data suggest that hybrid poplar plantations augmented with nest boxes may provide nesting habitat that is similar or superior to other habitats in North America. However the small sample size, isolated geographic location, and single year of data may not characterize all populations every year. Nevertheless, northern saw-whet owls can successfully nest in hybrid poplar plantations if nest boxes are provided.

Acknowledgements

Potlatch Corporation's Hybrid Poplar Program provided funding for this project. I thank M. C. Nowak for assistance in monitoring nests. In addition, I thank P. J. Heglund for reviewing and commenting on this manuscript.

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Received 29 January 2002
Accepted for publication 21 June 2002

Northwest Science Forum

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Robert T. Lackey,[1] National Health and Environmental Effects Research Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Corvallis, Oregon 97333

Salmon Recovery: Learning from Successes and Failures[1]

In this essay, I propose an answer to the question: What has been learned from 150 yr of efforts to protect and restore wild salmon in western North America?

Wild Pacific salmon in the lower 48 states are well on their way to attaining a status enjoyed by some of their notable brethren—wolves, condors, grizzlies, cougars, bison—wild animals that are unlikely to disappear entirely, but struggle to hang on as remnants of once flourishing species in limited portions of their original range (Lackey 2000). In California, Oregon, Idaho, Washington, and the Columbia River portion of British Columbia, many runs are reduced to <10% of their historical abundance. Some are much less than 10%. An unknown number have been extirpated (Lichatowich 1999).

Other salmon runs are dominated by hatchery-bred fish. Even for the Columbia, once the mightiest salmon-producing river south of Canada, over 80% of the total run comprises hatchery-bred fish (Lichatowich 1999). In the lower 48 states, fishing continues only because hundreds of hatcheries are able to keep runs at sufficiently high levels (Lackey 2000).

The chronicle of salmon decline in the Pacific Northwest is not unique. Of the Earth's four regions where Pacific and Atlantic salmon runs originally occurred, it looks increasingly like western North America will emulate the Asian Far East, Atlantic Europe, and eastern North America in having extirpated or much reduced runs in the southern portions of the distribution, and larger runs, closer to historical levels, in the northern portions.

When I look at the current status of wild salmon and apply common-sense, realistic assumptions, by 2100 the Pacific Northwest, south of mid-British Columbia, most likely will look like the U.S. portion of eastern North America, Europe south of Scandinavia, and the Asian Far East south of Russia. In all four regions, wild salmon runs likely will be a shadow of the past over much of the original range. Wild salmon runs in Alaska, Yukon, and northern British Columbia most likely will remain relatively healthy, or at least better off than those in the contiguous United States.

Such a forecast is not pleasing news for those who highly value wild salmon, nor is it pleasing news for those who do not rank salmon restoration

[1]Dr. Lackey (lackey.robert@epa.gov) is also a courtesy professor of fisheries and an adjunct professor of political science at Oregon State University. This essay is modified from a plenary lecture, Annual Meeting of the American Fisheries Society, Oregon Chapter, Sunriver, Oregon, 27 February-1 March 2002. The views and comments expressed are those of the author and do not necessarily represent those of any organization.

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as exceptionally important when compared with other societal needs. From their perspective, continuing the current salmon restoration policy wastes too much money, causes unnecessary social strife, and perpetuates a band of lawyers, lobbyists, and technocrats to act as policy mercenaries, all for a policy objective that many experts think probably will not be successful (Buchal 1998).

Policy Context

How did the Pacific Northwest get into this apparent conundrum in which no political faction is happy? The answer is embedded within past and current policy contexts. Let me describe a few points in salmon history from a policy perspective.

The year 1848, 154 yr ago, marked the beginning of the downward spiral for salmon in western North America (Lackey 2000). The precise date was 24 January 1848, the day gold was discovered near John Sutter's Sawmill overlooking the Central Valley of California. Gold mining proved to be a singularly salmon-unfriendly activity. Mining operations expanded rapidly to the watersheds surrounding the Central Valley, and the effect on salmon runs was immediate, massive, and obvious.

So began the decline of wild salmon that soon spread across the region. Mining was not the only human activity that adversely affected salmon. Fishing, farming, grazing, logging, diking, dredging, filling, clearing, building, constructing, paving, polluting, damming, diverting, channelizing, irrigating, and many other human enterprises, all contributed to the decline of salmon runs (Lichatowich 1999, Taylor 1999).

A century and a half of experience with managing salmon runs should reveal some general patterns, a few principles, and a handful of lessons learned — those that are likely to remain relevant through the current century. I will propose five lessons that are central to understanding the salmon decline and especially public policies concerning salmon recovery.

Policy Lesson 1—Policy Goals Are Fleeting

Perhaps most obvious, and arguably the most important lesson is the realization that salmon policy goals tend to be fleeting. Societal priorities are dynamic, difficult to forecast, subject to rapid change, and, perhaps most frustrating to technocrats, impossible to quantify accurately. Remember how the recent Pacific Northwest drought and California electrical blackouts affected thinking and priorities? Or even more recently, how the terrorist attacks of 11 September 2001, have so drastically recalibrated society's collective priorities? Let me recap the past 150 yr and identify a few examples of implicit public policy goals and priorities for salmon restoration.

By 1880, supplemental stocking for hatcheries was generally viewed as the solution to declining salmon runs (Lichatowich 1999, Scarce 2000). By the beginning of the 20th century, in public policy debates, hatcheries had won out over preserving or restoring natural habitat, and hatchery-bred fish had won out over wild salmon. Little more than a century later, protecting wild salmon is the preeminent statutory dictum (Taylor 1999, Lackey 2001a). Now hatchery bashing is in vogue, and it is hatcheries that are under siege as the nemesis of wild salmon runs. There is even discussion about closing some, or even all, salmon hatcheries (Buchal 1998).

A half century later, in the 1930s, the mantra was "put people to work to combat the devastating social effects of the Great Depression." Massive public works projects, such as many of the high dams of the Columbia River Basin were built, even though their ruinous effect on salmon was well known. A single dam, Grand Coulee, completely and permanently blocked a third of the Columbia Basin to migratory salmon — 1,600 km of the mainstream river lost to salmon in a single action. The Depression and public works projects won out over salmon. Now we are less sure of the priorities and we continue to spend millions trying to compensate for this lost spawning and rearing habitat.

Another half century later, in 1991, the first salmon distinct population segment or evolutionarily significant unit was listed under terms of the Endangered Species Act. With this action, the policy debate shifted away from restoring salmon runs to support harvest and fishing, to protecting salmon runs from extinction, two very different policy objectives (Lackey 2001a). A century ago few people cared much whether a salmon started life in a hatchery or in a redd. Now hatchery-produced salmon are not the restoration solution, they are part of the restoration problem, at least according to many.

In 2001, just a decade after the first Endangered Species Act salmon listing, a severe drought, combined with ongoing California electrical

blackouts, provoked the Bonneville Power Administration to declare a power emergency, abandon previously agreed upon interagency restoration commitments, and generate electricity using water reserved to facilitate salmon migration. In one of the most striking recent barometers of competing societal priorities, electricity won out over salmon, and with scant public opposition.

None of these public policy decisions over the past 154 yr was inherently good or bad; each simply reflected the priorities or legal interpretations of its time. We should accept that salmon policy goals have been fleeting and it seems apparent to me that 150 yr from now, society's salmon priorities will be as different as today's are from those of 150 yr ago.

Policy Lesson 2—Time Scales Rarely Coincide

When salmon biologists talk about restoring salmon runs, they tend to look at a 50 yr time span; a 100 yr time span is even better from their perspective. It is not that salmon biologists do not want to be helpful, but we are tempered, even constrained, by what we know to be ecological reality. Recent studies have confirmed what salmon biologists have long assumed: because of shifting climatic and oceanic conditions, the abundance of salmon varies naturally and considerably over decades and centuries (Finney et al. 2002).

Bureaucrats, on the other hand, work on much shorter time scales. They must enforce the controversial, restrictive, and often unpopular provisions of laws or court judgments. A decade is too long to wait for a definitive decision, let alone 50 or 100 yr. Policy decisions will be made with the best available science, but such science may be little more than an educated guess (Buchal 1998).

Elected officials, from a scientist's perspective, operate on comically short time-frames, something less than the interval between elections, often less than 2 yr. Some advocacy groups see declining salmon runs and demand immediate, decisive action from elected or appointed officials. Others, probably the majority, see abundant hatchery fish, paid for by license holders, electricity users, and taxpayers, and demand that they be allowed to fish. Understandably, in these circumstances policy decisions are made with whatever science is available and usually without much appreciation of its high degree of uncertainty.

Although many participants in salmon policy debates cast restoration decisions as science-based or science-driven, the reality is that such short decision time-frames constrain the role science plays. In practice, the so-called best available science is often that portion of scientific knowledge that can be construed to buttress the desired policy preference.

Policy Lesson 3—Scientists Are Essential, But Supporting Players

Let me invoke a trite, but useful theatrical metaphor: in the salmon restoration play, scientists, in their role as science-providers, are essential, but supporting players. It is not scientists' values and priorities that drive salmon policy, but those of society. Nevertheless, it is also true that a restoration strategy needs to be based on ecological reality, hence the essential role for science. Scientists are essential, not because they may advocate particular public policy priorities, but because they can provide society with the best assessment of ecological reality (Lackey 2001b). Do not assume that this is obvious and unassailable. It is not.

Most of us salmon technocrats struggle to accept the reality that there is no *scientific* imperative to restore wild salmon (Scarce 2000). But, there are also no scientific imperatives to keep energy costs low, to protect salmon gene pools, or to assert that maintaining runs of wild salmon is inherently a more desirable policy objective than using hatchery-reared salmon.

I am arguing for a clear, clean, conspicuous separation of science and decision-making, but I acknowledge that such a dichotomy is often ambiguous. But, as a guidepost, elected officials, not technocrats, have the political mandate to balance competing priorities. As we learned in college, fisheries management is mostly about people and their behaviors, not about fish.

Policy Lesson 4—Decision Optimization Is Naive

The fourth policy lesson was not intuitive to me: an infatuation with decision optimization is naive. Our professors taught us that to achieve public policy objectives, we should manipulate decision variables to produce maximum benefits for society.

Successful fisheries management, at least according to our classic natural resource management training, is typified by calls for efficiency, maximization, optimization, goals, objectives, performance measures, and monitoring (Scarce 2000). We instinctively seem to gravitate to maximum sustainable yield, optimum sustainable yield, maximum economic yield, maximum net economic benefit, maximum social benefit, and a mish-mash of related management targets.

It is nearly impossible to isolate and measure the things that are really important to people relative to salmon restoration. For example, how do you measure the tradeoff between using water to grow potatoes vs. using the same water to grow salmon? How important to fishermen are salmon that spawned in the wild vs. salmon that started life in a hatchery? How important is preserving the icon status of wild salmon vs. preserving private property rights? The important decisions in adjudicating salmon policy are driven, not by deference to efficiency, not by infatuation with optimization, not by devotion to management algorithms, but by passion, and passion comes from the heart, not from the latest, fastest computer chip driving the most elegant, dazzling software.

This lesson, that we technocrats must temper our penchant and infatuation with decision optimization, is difficult for many of us to accept. Decision optimization may work well on narrow, constrained, highly simplified decision problems, but not for the big, important, complex, divisive policy problems — such as reversing the decline of wild salmon.

Policy Lesson 5—Reality is an Orphan

In many debates over salmon policy, reality is often a casualty, an orphan. By reality, I mean that which is true, or at least that which is most likely to be true. I will define reality here as the facts of the case, the unvarnished reporting of the situation, the truth as it is, not as we might wish it to be.

In adjudicating salmon policy, reality often does not have a champion, a cheerleader, a proponent (Lackey 2001b). Most organizations that fund the development or dissemination of salmon information have a policy objective or at least a policy slant or bias (Buchal 1998). For example, these organizations typically may be in favor of increasing the sale of fishing licenses; or protecting the well-being of farmers, dam operators, or stockholders; or assuring that adequate and inexpensive electricity; or enhancing windsurfing, white water rafting, or snowboarding opportunities; or obtaining grants to keep their personal or institutional research adequately funded; or protecting imperiled species or habitats (Scarce 2000).

Problems with conveying reality are not limited to salmon scientists. What has been the response to the 2001 report from the Independent Scientific Advisory Board (2001) that judged, with a stunning jolt of candor, that none of the four Federal and state plans to restore wild salmon in the Columbia Basin will likely be successful? Surprisingly, there has been almost no reaction from the proponents and managers of the four plans, or from any other faction in the continuing salmon policy fray. Are the agency employees in the salmon restoration business worried about their jobs? If they are, it is unwarranted because, to my knowledge, no one has ever been fired because of failing to restore wild salmon.

Conclusion

I will end this essay with a prediction, and also offer a challenge: Any policy or plan targeted to restore wild salmon runs must at least implicitly respond to these policy lessons or that plan will fail. It will be added to an already long list of prior, noble, earnest, and failed restoration attempts.

Imagine the end of this century, less than 10 decades away, only a few dozen generations of salmon beyond today's runs, just two or three Pacific Decadal Oscillations from now, a time when this region's human population will not be its present 15 million, but rather will be somewhere between 50 and 100 million (Lackey 2000). As we move through this century, there are salmon restoration options that are likely to be ecologically viable and probably socially acceptable, but the range of restoration options continues to narrow.

In my view, as one of society's fisheries experts, it is a time for neither crippling pessimism, nor delusional optimism. Rather, it is a time for uncompromising ecological realism and forthright policy analysis. Society deserves no less from us.

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Lance W. Smith,[1] National Marine Fisheries Service, 525 NE Oregon St., Suite 500, Portland, Oregon 97232

A Framework of Ecosystem Processes for Evaluating Effects of Dams on Endangered Species

Introduction

The motivation to develop the process-based framework described in this paper was the listing of several species of freshwater and anadromous fishes under the Endangered Species Act (ESA) in the Willamette Basin, western Oregon (Figure 1) during the 1990s by the U.S. Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (NMFS). Unlike the Columbia River, the mainstem Willamette River is free of dams, nevertheless the construction and operation of large dams in the five major tributary subbasins (Figure 1) is one of the primary factors in the decline of the listed fish species (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2000, 2001). In the upper Willamette Basin, the

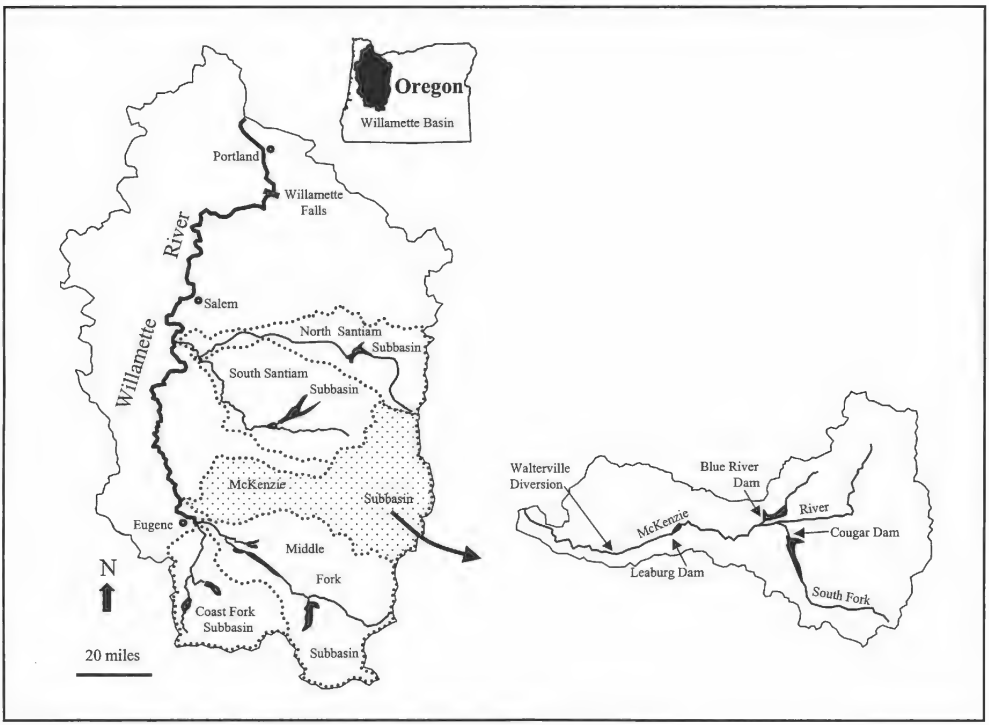

Figure 1. Map of the Willamette Basin and the four projects in the McKenzie subbasin.

[1]Current Address: Zoology Department, University of Hawai'i at Manoa, 2538 McCarthy Mall, Edmondson Hall, Honolulu, HI 96822 lancesmi@hawaii.edu

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U.S. Army Corps of Engineers (USACE) owns and operates 13 large multipurpose dams, while the Federal Energy Regulatory Commission (FERC) regulates several other privately owned large dams and diversions that are operated for hydroelectricity.

Under the ESA, NMFS manages listed species that spend most or all of their life cycle in the marine environment (e.g. anadromous salmonids), while USFWS manages listed species that spend most or all of their life cycle in the freshwater or terrestrial environment. Thus both agencies are involved in implementing the ESA in the Willamette Basin. The ESA requires federal agencies such as USACE and FERC that own, operate, permit, or fund existing dams to provide biological assessments on how the dams affect ESA-listed species to either NMFS or USFWS, depending on the species. NMFS or USFWS reply with a biological opinion describing the likely effects of the dams on listed species, and possibly including guidance on modifications to the structure or operation of the dams to reduce impacts on the listed species (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998). This exchange of biological assessments and opinions is referred to as an ESA consultation.

A Framework of Ecosystem Processes

Biological assessments and opinions on dams are best conducted within an ecosystem context that recognizes the fundamental role of hydrology, geomorphology, and water quality (habitat processes) to create and maintain habitat for individual species within a fluvial ecosystem (Independent Science Group 1996). The typical purpose of biological assessments and opinions is to determine how the construction or continued operation of a dam will affect one or a suite of species. An ecosystem context is critical to provide the framework for these species-specific analyses because: (1) dams alter the habitat processes upon which aquatic ecosystems are based, thus dams can have complex ecosystem-wide effects that may be overlooked if individual species are the sole focus; (2) recognizing the underlying habitat processes that support all associated species reduces the likelihood of a multispecies biological assessment or opinion pitting the perceived needs of one species against another; and (3) fluvial species evolved in spatially and temporally diverse ecosystems, rather than under stable conditions that have often been considered optimal. Based on these principles, a framework of relevant habitat and biological processes (together referred to as ecosystem processes) for the stream channels, riparian areas, and floodplains above Willamette Falls (the upper Willamette fluvial ecosystem) was developed to organize and guide ESA consultations on the continued operation and maintenance of dams in this area.

The top panel of Figure 2 illustrates the framework of ecosystem processes (i.e., combination of habitat and biological processes) in general for aquatic species within the upper Willamette fluvial ecosystem. The interlocking ovals symbolize the connectivity of the habitat processes with one another, and of the organism-level biological processes with one another. For example, disturbance and flow regime are different aspects of hydrology, with disturbance representing extreme but infrequent high flows, and flow regime representing mean flow patterns throughout the year. The arrows symbolize how the different processes generally influence one another. While some biological processes exert influence over some habitat processes (e.g., decomposition of salmon carcasses affects water quality), habitat processes generally exert more influence over organism-level biological processes. Likewise, organism-level biological processes exert more influence over population-level biological processes than vice-versa, and so on (Spence et al. 1996). The bottom panel of Figure 2 illustrates some of the linkages between habitat processes and the biological processes for listed spring chinook salmon in the upper Willamette fluvial ecosystem. The collective effects of habitat processes on each of the organism-level biological processes influence the function of population-level and community-level biological processes.

Application of the Ecosystem Framework

The framework of ecosystem processes shown in the top panel of Figure 2 provides the organizational basis for biological assessments and opinions on the effects of dams that may be applied to a wide range of spatial scales, temporal scales, species, and types and numbers of dams. As described in the example below, the framework has been applied to ESA consultations jointly carried

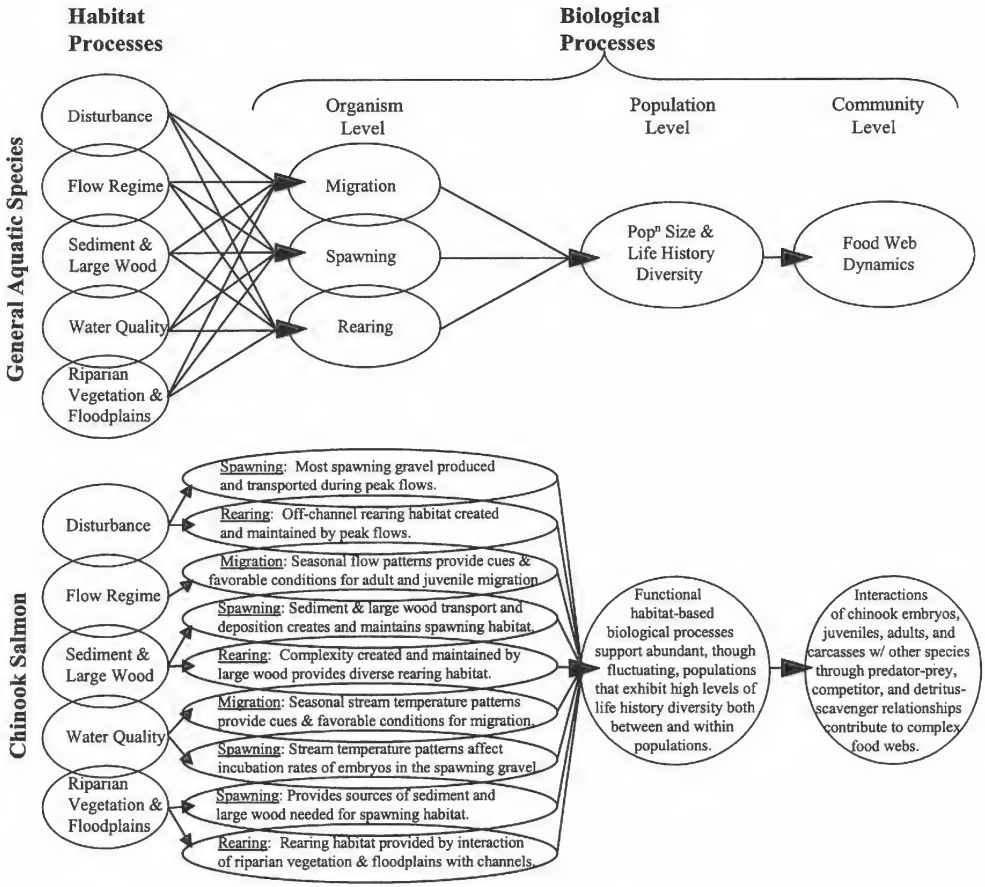
Habitat Processes
Biological Processes
Organism Level
Population Level
Community Level
General Aquatic Species
Disturbance
Flow Regime
Sediment & Large Wood
Water Quality
Riparian Vegetation & Floodplains
Migration
Spawning
Rearing
Popn Size & Life History Diversity
Food Web Dynamics
Chinook Salmon
Spawning: Most spawning gravel produced and transported during peak flows.
Rearing: Off-channel rearing habitat created and maintained by peak flows.
Migration: Seasonal flow patterns provide cues & favorable conditions for adult and juvenile migration.
Spawning: Sediment & large wood transport and deposition creates and maintains spawning habitat.
Rearing: Complexity created and maintained by large wood provides diverse rearing habitat.
Migration: Seasonal stream temperature patterns provide cues & favorable conditions for migration.
Spawning: Stream temperature patterns affect incubation rates of embryos in the spawning gravel.
Spawning: Provides sources of sediment and large wood needed for spawning habitat.
Rearing: Rearing habitat provided by interaction of riparian vegetation & floodplains with channels.
Functional habitat-based biological processes support abundant, though fluctuating, populations that exhibit high levels of life history diversity both between and within populations.
Interactions of chinook embryos, juveniles, adults, and carcasses w/ other species through predator-prey, competitor, and detritus-scavenger relationships contribute to complex food webs.

Figure 2. Framework of habitat and biological processes for aquatic species in general (top) and for chinook salmon (bottom).

out by NMFS and USFWS on the effects of dams in the McKenzie subbasin on the two listed fish species occurring there, spring chinook salmon and bull trout. The McKenzie subbasin contains two multipurpose dams owned and operated by USACE, located on the two largest tributaries of the Upper McKenzie River: Blue River Dam on Blue River and Cougar Dam on the South Fork McKenzie River (Figure 1). In addition, the Eugene Water and Electric Board (EWEB) owns and operates Leaburg Dam and Walterville Diverion on the lower mainstem of the McKenzie River, collectively called the Leaburg-Walterville Project, which is licensed by FERC. Leaburg Dam and the unscreened Walterville Diversion divert over half of summertime flows from the lower McKenzie River into the Leaburg-Walterville canal system. Collectively, these four projects have greatly altered fish habitat and fish passage in the McKenzie subbasin, contributing strongly to the decline of listed spring chinook salmon and bull trout (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2000, 2001).

NMFS and USFWS completed a draft joint biological opinion in late 2000 on the effects of the 13 USACE multipurpose dams in the upper Willamette, including Cougar and Blue River Dams, on listed species (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2000). NMFS and USFWS also completed a final

joint biological opinion in September 2001 on the effects of the Leaburg-Walterville Project on spring chinook salmon and bull trout (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2001). Both joint biological opinions applied the framework of ecosystem processes to determine the likely effects of the four projects on the two species over the next 10-50 yr. This information was then used in the biological opinions as the basis for remedial measures for USACE and FERC/EWEB to implement, so that the projects would comply with the ESA.

An example is described below of how the ecosystem framework was applied in the two biological opinions to determine the effects of the projects on a listed species. For brevity, the example traces the effects of the four projects in the McKenzie subbasin on only two habitat processes (flow regime, and sediment and large wood) for one listed species, spring chinook salmon. After the appropriate spatial and temporal scales were set, the framework was implemented in the following three steps: (1) the likely effects of the projects on the two habitat processes were determined; (2) based on effects to the two habitat processes, the likely effects on each biological process for spring chinook salmon were determined; and (3) the direct effects on biological processes of spring chinook salmon unrelated to habitat processes were determined (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2000).

For Step 1, it was determined that the four projects likely will affect flow regime over the next several decades by collectively reducing peak flows during winter and spring throughout the lower McKenzie River, and increasing low flows during summer and fall in the river except for the 13 mile-long Leaburg-Walterville bypass reach where a substantial proportion of flow will be diverted. For sediment and large wood, it was determined that the two USACE dams likely will continue to trap in their reservoirs a large proportion of sediment and large wood produced by the upper McKenzie subbasin. In contrast, the Leaburg-Walterville project passes most medium to large sediment and nearly all large wood because Leaburg Dam is a run-of-river project and Walterville Diversion has no dam.

For Step 2, it was determined that the flow regime effects likely will impact the biological process of migration for spring chinook salmon by hindering downstream juvenile migration during late winter and early spring due to reduced flows. Upstream adult migration during early summer was not expected to be impacted by the flow regime effects because the increased flows by the USACE dams compensate for the reduced flows by the Leaburg-Walterville Project. The effects on sediment and large wood likely will impact the biological processes of spawning and rearing for spring chinook salmon by reducing spawning gravels, and by reducing the physical complexity of rearing habitat due to lack of large wood, respectively.

Step 3 was done after the effects on all habitat processes, and subsequent effects on biological processes, were considered. For spring chinook salmon, the direct effects of the four projects on fish passage (i.e., the physical blocking of passage by the dams) are not related to habitat effects. The USACE dams lack passage facilities, and thus block spring chinook salmon from a large proportion of historic habitat, especially above Cougar Dam. Leaburg Dam and Walterville Diversion both kill 10-15% of outmigrating spring chinook fry, while Leaburg Dam delays adults. Based on the expected effects outlined in Steps 2 and 3, proposed remedial measures included increasing water releases from the USACE dams in the spring, a hydrogeomorphic study to better determine effects of the four projects on sediment and large wood, passing some large wood around the USACE dams, designing fish passage facilities for Cougar Dam, improving fish passage facilities at Leaburg Dam, and installing a fish screen at the Walterville Diversion (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2000, 2001).

Institutional Barriers

Four institutional barriers within NMFS and USFWS hinder the implementation of an ecosystem framework for evaluating the effects of dams. First, NMFS and USFWS share jurisdiction under the ESA, depending on whether the listed species is marine, freshwater, or terrestrial. The development of the joint Endangered Species Consultation Handbook (USFWS and NMFS 1998) helped to unify the efforts of the two agencies, but joint ESA consultations are still uncommon on projects affecting species under the

jurisdiction of both agencies. Second, physical processes such as geomorphology and hydrology are not given due consideration by NMFS and USFWS in the conservation of aquatic species. For example, as of April 2002, NMFS employed over 100 biologists in Oregon, Washington, and Idaho to conduct ESA consultations and other environmental regulatory work on in-channel activities such as dams, roads, bridges, and dredging. However, NMFS only employs one physical scientist (a hydrologist) in the entire region to assist the biologists in interpreting the effects of such activities on physical processes.

Third, NMFS and USFWS staff have poor information resources at their disposal. Agency managers are pressured by litigation and politicians to complete biological opinions quickly, but staff lack the information they need to do the job accurately within the desired time frame. For example, neither of the largest NMFS and USFWS offices in the Pacific Northwest (both in Portland, Oregon) has a library or information management staff. Fourth, NMFS and USFWS have focused on the effects of single, small-scale human activities on individual organisms, while often ignoring the effects of multiple activities at large scales on populations and species. Several factors are involved in this phenomenon, including the complexity of cumulative effects at large scales, and the desire of staff to work on projects they can most easily understand and control. The resulting institutional myopia hampers an ecosystem approach to implementing the ESA.

Recommendations

The following recommendations help implement an ecosystem framework for biological assessments and opinions on the effects of dams or other in-channel activities on vertebrate, invertebrate, and plant species. Inherent in the recommendations is an interdisciplinary approach that may require environmental regulators to integrate unfamiliar subject matter into their areas of expertise.

1. Define the area of interest hydrologically, such as a watershed or basin, plus downstream streams, channels, and floodplains.
2. If there is more than one dam within the area of interest, synthesize evaluations of the effects of each dam into a comprehensive evaluation so that combined effects are not overlooked.
3. Work with sister agencies that have jurisdiction within the area of interest to produce joint evaluations of the effects of dams on a suite of species.
4. Identify spatial and temporal scales for the evaluation, based on the estimated geographic and temporal extent of the effects of the dams, the range of protected species or populations, and policy, legal, and management considerations.
5. Establish a framework of ecosystem processes relevant to the watershed (habitat processes) and species (biological processes) of interest to guide the evaluation effort.
6. Determine the status of the ecosystem processes for the watershed and species of interest. Obtaining the best available information requires patiently contacting agency staff and sifting through the gray literature, and the more straightforward review of the scientific literature.
7. Predict the likely effects of the dams on the habitat processes at the specified spatial and temporal scales. This interdisciplinary exercise requires staff to integrate hydrology, geomorphology, riparian function, floodplain ecology, and water quality to form a complete picture of the effects of the dams on the underpinnings of the fluvial ecosystem.
8. Based on the likely effects of the dams on the habitat processes, predict the likely effects on the biological processes of each species considered in the biological evaluation. In addition, consider the effects of the dams on biological processes not related to effects on habitat processes (e.g., direct effects of dams on fish passage may be unrelated to the effects of dams on habitat processes).

In conclusion, it is an impossible task to predict the *actual* biological effects of a complex human activity (operation of dams) in a complex ecosystem (the fluvial ecosystem) with a high level of certainty, especially if the biological evaluation is on a little-studied species. However, by first establishing a context of how the dams affect habitat processes, and then considering the biological processes of each species in question within this habitat context, the *likely* biological effects can be determined. The integration of habitat processes and biological processes at the appropriate spatial and temporal scales establishes a meaningful framework of ecosystem processes for evaluating the likely effects of dams.

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Spence, B. C, G. A. Lomnicky, R. M. Hughes, and R. P. Novitzki, 1996. An Ecosystem Approach to Salmonid Conservation. Mantech Technology, Corvallis, Oregon.

U.S. Fish and Wildlife Service and National Marine Fisheries Service. 1998. Endangered Species Consultation Handbook: Procedures for conducting consultation and conference activities under Section 7 of the Endangered Species Act. March 1998 Final. U.S. Government Printing Office, Washington, D.C.

NORTHWEST SCIENCE

Information for Authors

Purpose and Scope

The Northwest Scientific Association represents the natural and social sciences in the Pacific Northwest. The pages of *Northwest Science* are open to original and fundamental research in the basic and applied natural and social sciences. All submissions are refereed, usually by two reviewers and an Associate Editor. Papers are welcome from authors outside of the Pacific Northwest.

Web Site Information

Authors should visit the Northwest Scientific Association web site to obtain the most recent version of Information for Authors. The web site address is: www.vetmed.wsu.edu/org_NWS/NWSci_Home.htm

Articles

Articles present the results of new and original research, and generally are 6–20 journal pages long. Authors must contact the Editor in advance before submitting longer papers. Authors are encouraged to use line numbering for the original submission, which will help speed up the review process.

Notes

The purpose of Notes is to publish papers typically less than five journal pages long. Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for Notes, but all will be peer-reviewed and must be scientifically creditable. Authors may contact the Editor about the suitability of manuscripts to be published as Notes.

Northwest Science Forum

This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

Manuscripts

General Instructions

Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point Times New Roman font, on 8.5" x 11" paper, double-spaced throughout (including Abstract, Acknowledgements, Literature Cited, Tables, and Figure captions). Allow one-inch margins around the page. The format and style of manuscripts should conform to general usage in recent issues, and should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgements)
- Literature Cited
- Footnotes
- Tables
- Figure Captions
- Figures

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In that situation, lowercase letters will be used. Do not hyphenate words at the ends of lines. Words to be italicized will be typed in italic rather than underlined.

Title Page

The first page of the manuscript should contain:

- Author name(s)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running footer (for right-hand pages)
- Total number of tables and figures
- List the name, full address, telephone number, fax number, and e-mail address of the author to whom correspondence should be sent. Use a footnote to indicate a corresponding author other than the senior author. For example: "[1]Author to whom correspondence should be addressed."

Abstract

The second page of the manuscript contains the Abstract. Authors are strongly encouraged to give the abstract proper attention. The abstract briefly summarizes the study, so that it is quickly accessible to the general readership of the journal. The abstract must be written in complete sentences and may not exceed 250 words. Because of the diverse disciplines and readership served by the journal, the abstract should include the following three parts: 1) a statement of the purpose of the study, indicating the reasons behind its undertaking; 2) a statement describing the experimental design or approach and a summary of the results; 3) a summarizing sentence or two regarding the larger significance of the research.

Text

Start the text on the third page, and use continuous pagination. Do not start new sections on new pages.

Literature citations within the text should contain the author's name and year of publication, using formats A and B. Multiple citations of authors within the same parentheses will be listed in chronological order.

- Format A:

  ...studied by Jones (1998)...

  ...studied by Smith and Brown (1999)...

  ...studied by Smith et al. (2000)...(if more than two authors in a citation)

- Format B:

  ...was previously investigated (Smith 1991, Jones 1995, Harris 2000)

  ...results of other investigations (Smith 1991, 1995; Jones 1993; Brown 1999)

Numbers from one to nine will be spelled out, while Arabic numerals will be used for numbers 10 and larger. Exceptions to this convention are: 1) a series of mixed numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 5 g, 0.7 mm, 3 m^2). Arabic numerals will also be used for dates, times, page numbers, and percentages.

Authors are requested to use the International System of Units (SI). Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1998). Use leading zeroes with all numbers <1 (e.g., 0.12), including probability values with "*P*" capitalized and italicized (e.g., $P \leq 0.05$). Please note these examples of other conventions followed by *Northwest Science*: 20th Century, 3rd Edition, Douglas-fir, dbh, sec, min, hr, day (or d), wk, mo, yr. Please do not use the construction "and/or" because "or" invariably will suffice.

On first mention in the text, a species should be designated by common name followed by systematic binomial (italicized). If a common name is available, systematic binomials are unnecessary, and are not recommended, in the Title and Abstract. Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." In general, authors should follow conventions for their disciplines (e.g., botany, ornithology). Consult with the Council of Biology Editors *CBE Style Manual*, 4th ed., for general information on manuscript preparation.

Personal Communications

These should be kept to an absolute minimum, because they do not meet the requirements for first disclosure as defined by the Council of Biology Editors. If used, the full name and affiliation of the person being quoted is required. *Personal communications are cited in the text,* not in Literature Cited. For example:

... (David L. Peterson, University of Washington, personal communication).

Literature Cited

Only the *first letter* of the *first word* of journal articles, technical reports, theses, symposia papers, and technical bulletins are capitalized. First letters of *major words* in book titles are capitalized. All authors and editors of a title will be listed in the bibliographic citation. Use "et al." only in the body of the text, never in the Literature Cited section.

Citations should be double-spaced and listed in alphabetical order at the end of the article. *Note that the names of all sources are spelled out.* The only exceptions are the commonly used abbreviations USDA, USDI, EPA, and USA. The abbreviations USDA and USDI must be followed by the name of the agency (e.g., USDA Forest Service; USDI Bureau of Land Management).

Double-check literature to ensure that citations in the text and in Literature Cited agree. On one submitted copy, indicate by green check marks on each citation in the text and each citation in Literature Cited that the references have been double-checked.

The general format for citations is:

- Last name, initials of the first name and middle name, then switch to initials followed by the last name for subsequent authors.
- Use a space between initials and names.
- Short bar. Beginning with the Fall 2001 issue, *Northwest Science* will no longer use a short bar for repeated entries by the same author.
- Issue numbers are unnecessary.
- Double-check each citation to ensure that it conforms to the *Northwest Science* format.

Typical examples of *Northwest Science* format conventions for Literature Cited are as follows:

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus*. Journal of Mammalogy 51:310-326.

Broadbooks, H. E. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus*. American Midland Naturalist 83:472-488.

Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Edmunds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York. *(number of pages unnecessary)*

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393 *In* H. Barnes (editor), Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

Theses, dissertations, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary ponds in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. Ph.D. Dissertation, University of Utah, Salt Lake City, Utah.

Dunwiddie, P. W. *In Press*. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science. *(if the publication date is unknown or uncertain)*

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: *(in press). (if the publication date is known and certain).*

Technical bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Online (web) references

USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

Unpublished Reports

Unpublished reports often contain useful data that contribute to the development of the study being

reported. Even though they do not meet the criteria for first disclosure, if they have a date, author, and a location where the report is on file, so that interested readers can obtain a copy of the report, they may be listed in Literature Cited so that the text reads more smoothly. If the date is unknown, treat the report as a personal communication and cite it in the text. If the location is unknown, do not use the report.

Kraft, G. F. 1967. Annual report on the status of Lake Whatcom. Unpublished report on file at Western Washington University, Bellingham, Washington.

Footnotes

Footnotes to the text are discouraged. In most cases, the potential footnote information can easily be incorporated in the text. If footnotes are unavoidable, they must be numbered consecutively and clearly indicated in the text.

Tables

All tables must be cited in the text, but typed and double-spaced on separate pages. Set up tables using tab stops; do not use auto-formatted tables. Note that the word "Table" is in all caps at the beginning of the TABLE caption, but in lower case in the text. When submitting tables electronically, *they should be presented in the simplest tabular format possible*, and placed after the body of the manuscript. Use letters as superscripts to indicate statistical differences among values being compared (numbers with different letters indicate significant differences at $P \leq 0.05$) Footnotes to tables are numbered consecutively with each table treated as a separate entity (i.e., the first footnote on each table should be 1).

Figures

All figures must be cited in the text. To achieve highest quality reproductions, it is preferable for the printer to work directly from photographs or original drawings. Thus, original artwork or 5" x 7" (or larger) black & white glossy prints of photographs must be submitted for reproduction. Mount photos on lettering board to protect them from damage. Artwork and lettering should be large enough (but not overly large) to provide clarity after a 50% reduction in size for printing. *The author's name, figure number, and indication of "top" should be penciled on the back of each illustration.* Illustrations of study areas should include a small inset that locates the study area in the state or province. Provide a scale for distance on map illustrations. Captions for illustrations should be typed as a group and placed on a separate page. The words Figure and Table will be spelled out in the body of the text, and capitalized as follows:

- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photos, and other illustrative material cannot be returned to the author.

Editing

The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

Submission of Final Copy

Manuscripts accepted for publication must be submitted in electronic copy and hard copy. Authors will receive instructions from the Editor regarding this procedure.

Publication Agreement

Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

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One set of page proofs will be sent to the corresponding author for correction shortly before publication. **Proofs must be returned to the Editor within three days of receipt—preferably by express mail.** Authors must inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs. Allow 8 weeks for delivery after the journal issue carrying the article appears.

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Page charges are currently $65 per printed page for members of the Northwest Scientific Association, and $80 for non-members. Authors wishing to become members may contact the Treasurer.

You must submit some form of payment with the order form and the proofs. It is not sufficient to request an invoice from the Association. Institutional checks, personal checks, money orders, and credit card orders are acceptable and should accompany the page proofs. **If an institutional purchase order is being used for payment, then the purchase order must accompany the page proofs.**

Correspondence

All correspondence regarding manuscripts will be between the corresponding author and Editor.

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The Editor and Associate Editors reserve the right to select reviewers of their choice.

Revised July 2002

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WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Presorted Standard
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*